## INTRODUCTION

Lizards of the genus *Draco,* by virtue of their pleasing and surprising wing coloration and ability to glide, have long attracted the attention of herpetologists. However, this attention has not often been translated into systematics research. Aside from Taylor's (1963) account of the species occurring in Thailand, the most recent review of the genus is Hennig's published in 1936. The collection in recent years of rather large samples from Borneo, Malaya, and Thailand provides an opportunity to evaluate intra- and interspecific variation, to consider the patterns of local morphological variation, and to present a body of ecological data.

The present review of morphological variation covers all species recognized by Hennig, although several appear to be conspecific. With respect to geographic coverage, samples have been available from most parts of the ranges of all species. The principal exceptions to that statement are geographically limited samples of *D. lineatus* and small samples from the Lesser Sunda portions of the range of *D. volans*.

While analysis of data collected for this study was under way, I learned of a review of the genus being undertaken by Mr. C. Musters at the Rijksmuseum in Leiden. We have exchanged views in correspondence, and Mr. Musters has generously sent me a copy of his manuscript. As our taxonomic opinions diverge significantly, it seems best that each of us publish his own data, analysis, and conclusion. If our science is self-correcting, readers and future workers can decide where each of us has made errors and take appropriate steps to correct them. To limit unnecessary duplication of topics included in Mr. Musters' manuscript, however, the present paper will not present keys, detailed descriptions, or details of geographic distribution. Instead, this paper will focus on patterns of morphological variation and ecological information. Summary of quantitative data on specimens examined in this study is presented in the Appendix.

This paper is dedicated to three colleagues at Field Museum, Henry S. Dybas (now deceased), Melvin A. Traylor, and Rupert L. Wenzel, who have encouraged and stimulated me and offered sound advice for more than 30 years.

## MATERIALS AND METHODS

### Specimens Examined

Material studied is listed below by species as recognized in this paper. Standard abbreviations (Leviton et al., 1980) are used for names of institutions.

*bimaculatus:* Leyte 1 (FMNH); Samar 2 (FMNH); Mindanao 30 (CM 13, FMNH 17); "Philippine Islands" 1 (BM, holotype).

*blanfordi:* Burma 2 (BM, types); Thailand 38 (BM 4, including holotype of *cyanolaemus,* FMNH 16, MCZ 1, USNM 17); West Malaysia 3 (BM).

*cristatellus:* Thailand 4 (BM 1, Boonsong collection 2, MCZ 1); West Malaysia 2 (BM);

Sumatra 3 (BM 1, MZB 2); Mentawei Islands 1 (BM); Borneo 7 (BM 2, holotype of *cristatellus* and paratype of *punctatus*, FMNH 4, MCZ 1).

*dussumieri:* India 20 (CAS 1, FMNH 19).

*fimbriatus:* Thailand 11 (AMNH 2, BM 2, FMNH 5, USNM 2); West Malaysia 15 (BM 7, FMNH 7, USNM 1); Singapore 1 (BM); Natuna Islands 1 (USNM). Sumatra 6 (FMNH); Borneo 7 (AMNH 1, FMNH 4, MCZ 2); Java 9 (RMNH 4, USNM 5); Ceram 1 (USNM).

*haematopogon:* Sumatra 7 (FMNH); Borneo 58 (BM 2, including holotype of *microlepis*, CAS 8, FMNH 47, MCZ 1).

*lineatus:* Celebes 19 (BM 1, holotype of *spilonotus*, FMNH 18); Amboina 21 (FMNH).

*maculatus:* Hainan 1 (FMNH); Indochina 5 (FMNH); Thailand 83 (CAS 22, FMNH 61).

*maximus:* West Malaysia 9 (FMNH); Borneo 67 (BM 1, holotype, FMNH 64, MCZ 1, UMMZ 1).

*melanopogon:* Thailand 9 (USNM); West Malaysia 323 (FMNH 302, USNM 21); Borneo 1,077 (FMNH 1,070, MCZ 5, USNM 2).

*mindanensis:* Mindanao 13 (CAS 4, FMNH 4, MCZ 4, USNM 1, holotype).

*obscurus:* Borneo 170 (BM 1, holotype of *obscurus*, FMNH 168, MCZ 1); West Malaysia 45 (BM 1, holotype of *formosus*, CAS 2, FMNH 42); Thailand 5 (FMNH 2, MCZ 2, USNM 1).

*quinquefasciatus:* Thailand 1 (USNM); West Malaysia 36 (BM 1, holotype, FMNH 35); Natuna Islands 1 (USNM); Sumatra 3 (USNM); Banka 1 (USNM); Karimata 1 (USNM); Borneo 873 (MCZ 4, FMNH 864, UMMZ 1, USNM 4).

*taeniopterus:* Thailand 45 (FMNH 20, USNM 25).

*volans:* Thailand 25 (BM 4, FMNH 3, USNM 18); West Malaysia 59 (BM 3, FMNH 53, USNM 3); Singapore 8 (FMNH); Sumatra 15 (BM 2, FMNH 8, USNM 5); Nias 4 (BM); Natuna Islands 4 (BM 1, USNM 3); Java 48 (BM 3, FMNH 12, USNM 33); Borneo 131 (AMNH 7, BM 6, including 2 syntypes of *cornutus*, FMNH 94, MCZ 24, including paratype of *gracilis*); Palawan 10 (BM 4, FMNH 6); Jolo 8 (BM 2, USNM 6); Mindanao 44 (BM 1, syntype of *everetti*, CM 22, FMNH 21); Dinagat 1, (BM, syntype of *everetti*); Cebu 9 (FMNH); Negros 30 (FMNH); Bohol 1 (FMNH); Samar 18 (FMNH); Leyte 3 (BM 2, UMMZ 1); Sibuyan 17 (BM 2, syntypes of *quadrasi*, CM 15, FMNH 2); Marinduque 51 (CM); Lubang 18 (CM 16, FMNH 2); Luzon 14 (CAS 1, CM 5, FMNH 8); Batanes Islands 2 (FMNH); "Philippine Islands" 2 (BM, holotypes of *guentheri* and *reticulatus*); Celebes 2 (BM); Flores 6 (BM 5, FMNH 1); Lombok 1 (BM); Timor 2 (FMNH).

## Characters Studied

The characters are divided into three groups: mensural, meristic, and qualitative.

The mensural characters comprise:

Snout-vent length (SV): measured to the nearest 0.5 mm.

Head length (HL) as a proportion of SV: head measured to nearest 0.5 mm from tip of snout to rear of jaw.

Length of dewlap (DL) as a proportion of SV: measured to nearest 0.1 mm from tip of chin to tip of adpressed dewlap; although including more than the dewlap proper, the measure was defined in this way because the precise origin of the dewlap cannot always be determined externally.

Nasal scale (NA) as a proportion of SV: measured in its anteroposterior axis with an ocular micrometer at 12 ×; 12 micrometer units equal 1.0 mm.

Largest dewlap scale (DS) as a proportion of NA: measured in its longest dimension with an ocular micrometer at 12 ×.

Largest tympanic scale (TY) as a proportion of NA: measured in its anteroposterior axis with an ocular micrometer at 12 ×; at low magnification, both nasal and tympanic scales are visible in a microscopic field permitting rapid comparison.

Relative sizes of lowest lateral caudals and subcaudals (CA): combined length of three successive lateral caudals divided by combined length of three successive subcaudals; measured approximately two head lengths behind vent with an ocular micrometer at 12 ×.

The meristic characters include:

Number of ribs supporting patagium: counted on one side.
Number of supralabials (SL): counted on one side.
Number of scales touching rostral (RS), excluding supralabials.
Number of upper "incisors," small conical teeth between enlarged canine-like teeth: the "incisors" consist of the premaxillary teeth plus the first maxillary tooth on each side.
Number of nuchal crest scales: specialized scales laterally compressed with height equal to or greater than anteroposterior length; present in only a few forms.
Subdigital lamellae of fourth toe.

The qualitative characters include:

Orientation of nostril when animal viewed head-on: axis of nostril may be lateral (i.e., projection below canthal ridge), oblique (projection in line of canthal ridge), or dorsal (projection above canthal ridge).
Homogeneity of dorsal head scales.
Carination of scales on forehead: in some forms, large keeled scales on forehead form an inverted Y or an I.
Flexible supraciliary "horn," a specialized compressed scale higher than wide: not to be confused with inflexible conelike scale covering bony projection at rear of orbit.
Dewlap shape which varies among species: well illustrated by Hennig (1936).
Caudal crest: in a few species males have a mid-dorsal row of compressed raised scales on the tail; females of these species and both sexes of others lack a caudal crest.
Dorsal and ventral coloration of the patagium.

## Statistical Analysis

When local samples of a given species were large, say $N > 10$, numerical data were recorded for only 10 males of each such sample. Thus, in the case of *D. melanopogon*, which was represented by five local samples (three in Borneo and two in the Malay Peninsula), each of which had $N > 125$, statistical analysis was based on aliquots of the total sample seen, which still allowed for statistically adequate samples (see Appendix). Aside from the instances of large samples, quantitative data were recorded for all males examined and for a varying, usually smaller, proportion of females. In general, information was recorded on more females where problems arose in definition of species than in other taxa. The end result, however, has been reduction in quantitative information on females. This limitation, though deliberate, would have resulted in any case, because most samples seen contained a decidedly higher proportion of males,[1] which in turn probably is a function of their being more conspicuous to human hunters. Has this pro-male bias affected the analysis? It has certainly limited examination of sexual dimorphism within species (or populations). However, it has not affected esti-

[1]For example, males constituted 64% and 58% of the very large samples of *D. melanopogon* and *D. quinquefasciatus*, respectively, from Nanga Tekalit, Sarawak. In the small total samples of *D. fimbriatus* and *D. cristatellus*, males constituted, respectively, 64% and 75%.

mates of intraspecific variation in meristic characters, such as supralabials, which do not show sexual dimorphism. More importantly, the primary interspecific analysis has not been biased, as it was based solely on males (see below).

Standard statistical tests, described by either Siegel (1956) or Sokal & Rohlf (1969), were applied in most comparisons involving a single quantitative character. For comparisons among populations and species involving variation in a number of quantitative characters simultaneously, I used a principal components analysis (PCA) as described by Nie et al. (1975). As PCA utilizes correlations among characters, parametric statistics underlie it. The characters used in the present PCA were as follows: snout-vent, supralabials, incisors, scales bordering the rostral, length of dewlap, nasal, largest tympanic scale, largest dewlap scale, and sizes of caudal scales. We might assume the first four, being either counts or a measure, to have normal distributions, but the last five are ratios (see Characters Studied) whose distributions cannot be assumed to be normal and therefore might not be suitable for use in PCA. To resolve this issue, the distributions of these five were tested for departure from normality in the *D. melanopogon* sample, selected because of its size (N = 38 to 49). Four of the five did not differ significantly from normal distributions (chi-square tests, $P > .5$), whereas the fifth, that of the nasal, did (chi square = 29.8, df = 8, $P < .01$). This modest departure from the assumptions of parametric statistics probably has not affected the outcome of the PCA.

Only males were used in the PCA to avoid the complication of sexual dimorphism, to permit inclusion of characters relating to the gular dewlap, and to avoid possible bias resulting from limited information on females (see above).

## Ecological Data

Information on exact position at time of first sighting was recorded for over 2,500 individuals (comprising 10 species) collected at three locations in Borneo, two in West Malaysia, and one in northeastern Thailand. Although much more limited in quantity, sightings (but not captures) of five species were made from tree platforms (Bacon, 1970).

A limited examination of stomach contents was carried out using 25 individuals of each of three co-occurring species—*melanopogon, quinquefasciatus,* and *obscurus*—from Nanga Tekalit, Sarawak. To this sample were added the stomach contents of 14 *D. maximus* from Nanga Tekalit and 10 *maximus* from other localities at which the other three species also occur. Prey items were counted and measured by means of a grid fixed to an evaporating dish. The lengths of fragmented prey organisms were estimated by comparison with entire individuals of the same taxonomic category. As the taxonomic range of food items was very limited, this procedure has probably not resulted in important distortion.

## SPECIES RECOGNIZED

The abbreviated synonymies below are presented in order to tie the analysis of variation to the taxa of the literature. In addition to original citations, the synonymies include Hennig's designations. The abbreviated diagnoses are supplemented by data in the Appendix. The sequence of species is alphabetical.

**Draco bimaculatus** Günther

*Draco bimaculatus* Günther, 1864, Rep. Br. India, p. 127—Philippines.
*Draco lineatus bimaculatus* Hennig, 1936, Temminckia, **1**: 197.

*Diagnosis.* A small species, adults rarely over 70 mm SV; 5 ribs in patagium; nostrils pointing laterally; a large tympanic scale; 5 incisors; 83% with 8 or 9 supralabials; 72% with 5 or 6 scales bordering rostral; subcaudals usually 1.2–1.3 times length of adjacent scales; dewlap triangular, with small scales.

**Draco blanfordi** Boulenger

*Draco blanfordi* Boulenger, 1885, Cat. Lizards, **1**: 267—Tavoy, Burma; Hennig, 1936, op. cit., p. 214.
*Draco indochinensis* Smith, 1928, Ann. Mag. Nat. Hist., ser. 10, **2**: 248—Bockor, Cambodia.

*Diagnosis.* A large species, adults more than 100 mm SV; 5 ribs in patagium; nostril pointing obliquely; a large tympanic scale; 4 incisors; 68% with 8 or 9 supralabials; 77% with 7 or 8 scales bordering rostral; subcaudals usually 1.3–1.7 times length of adjacent scales; dewlap elongate, slightly swollen near end, covered with large scales; males with a low caudal crest.

**Draco cristatellus** Günther

*Draco cristatellus* Günther, 1872, Proc. Zool. Soc. London, **1872**: 592—Sarawak.
*Draco punctatus* Boulenger, 1900, Ann. Mag. Nat. Hist., ser. 7, **6**: 189—Larut Hills, Malaya and Sarawak; Hennig, 1936, op. cit., p. 182.
*Draco fimbriatus fimbriatus* Hennig, op. cit., p. 202 (part).

*Diagnosis.* A moderate-sized species, adults usually 70–90 mm SV; 5 ribs in patagium; nostrils pointing laterally or slightly obliquely; a large tympanic scale; usually 4, sometimes 5 incisors; 75% with 9 or 10 supralabials; 64% with 7 scales bordering rostral; subcaudals and adjacent scales subequal; dewlap triangular, tapering gradually, covered with small scales; males with low caudal crest. Two individuals, including the paratype of *punctatus* Boulenger, have 6 ribs in the patagium.

**Draco dussumieri** Duméril and Bibron

*Draco dussumieri* Duméril and Bibron, 1837, Erpet. Gén., **4**: 456—Malabar coast; Hennig, 1936, op. cit., p. 191

*Diagnosis.* A moderate-sized species, adults 70–90 mm SV; 6 ribs in patagium; nostrils pointing dorsally; a large tympanic scale; 4 incisors; 69% with 10 or 11 supralabials; 77% with 7 or 8 scales bordering rostral; subcaudals variable, from 1–1.75 times length of adjacent scales; dewlap elongate, tapering gradually to broad tip, scales slightly enlarged; males with low caudal crest.

**Draco fimbriatus** Kuhl

*Draco fimbriatus* Kuhl, 1820, Beitr. Zool. Vergl. Anat., p. 101—"India orientali."
*Draco fimbriatus fimbriatus* Hennig, 1936, op. cit., p. 202.

*Diagnosis.* A large species, adults usually more than 100 mm SV; 5 ribs in patagium; nostrils pointing laterally or slightly obliquely; a large tympanic scale;

4 incisors; 70% with 11 or 12 supralabials; 62% with 7 or 8 scales bordering rostral; subcaudals and adjacent scales subequal; dewlap tapering gradually to broad tip, covered with small scales; males with low caudal crest.

**Draco haematopogon** Gray

*Draco haematopogon* Boie in Gray, 1831, Griffiths Anim. Kingdom, **9**, Syn., p. 59—no type locality given; Hennig, 1936, op. cit., p. 204.
*Draco microlepis* Boulenger, 1893, Proc. Zool. Soc. London, **1893:** 523—Merabeh, Sabah.
*Draco haematopogon microlepis* Hennig, 1936, op. cit., p. 206.

*Diagnosis.* A small species, adults usually less than 80 mm SV; 5 ribs in patagium; nostrils pointing dorsally; a large tympanic scale; 4 incisors; 78% with 11 or 12 supralabials; 68% with 8 or 9 scales bordering rostral; subcaudals 1.2–1.6 times length of adjacent scales; dewlap elongate, triangular, tapering gradually, covered with small scales.

**Draco lineatus** Daudin

*Draco lineatus* Daudin, 1803, Hist. Nat. Rep., **3:** 298—Java; Hennig, 1936, op. cit., p. 194 (part).
*Draco spilonotus* Günther, 1872, Proc. Zool. Soc. London, **1872:** 592—Manado, Celebes.
*Draco lineatus spilonotus* Hennig, 1936, op. cit., p. 199.

*Diagnosis.* A small species, adults usually less than 80 mm SV; 5 ribs in patagium; nostrils pointing laterally; small tympanic scales; 5 incisors; 73% with 6 or 7 supralabials; 77% with 5–7 scales bordering rostral; subcaudals subequal to adjacent scales; dewlap triangular, tapering gradually, covered with small scales.

**Draco maculatus** (Gray)

*Dracunculus maculatus* Gray, 1845, Cat. Lizards, p. 236—Penang Island.
*Draco maculatus* Hennig, 1936, op. cit., p. 211.

*Diagnosis.* A small species, adults usually less than 80 mm SV; 5 ribs in patagium; nostrils pointing laterally; tympanic scales small; 4 incisors; 71% with 8 or 9 supralabials; 72% with 5 or 6 scales bordering rostral; subcaudals subequal to adjacent scales; dewlap elongate, tapering near base, tip broad, covered with small scales; males with low caudal crest.

**Draco maximus** Boulenger

*Draco maximus* Boulenger, 1893, Proc. Zool. Soc. London **1893:** 522—Mt. Dulit, Sarawak; Hennig, 1936, op. cit., p. 188.

*Diagnosis.* A very large species, adults 110–140 mm SV; 6 ribs in patagium; nostrils pointing dorsally; tympanic scales small; usually 4 incisors; 60% with 14 or 15 supralabials; 64% with 9 or 10 scales bordering rostral; subcaudals 1.3–2 times length of adjacent scales; dewlap elongate, tapering to narrow tip, covered with small scales.

**Draco melanopogon** Boulenger

*Draco melanopogon* Boulenger, 1887, Cat. Lizards **3:** 492—Malacca, Malaya; Hennig, 1936, op. cit., p. 207.

*Diagnosis.* A moderate-sized species, adults 70–85 mm SV; 5 ribs in patagium;

nostrils pointing dorsally; a large tympanic scale; 4 incisors; 61% with 12 or 13 supralabials; 69% with 9 or 10 scales bordering rostral; subcaudals 1.3–2 times adjacent scales; dewlap elongate, tapering only near base, scales slightly enlarged.

**Draco mindanensis** Stejneger

*Draco mindanensis* Stejneger, 1908, Proc. U.S. Nat. Mus., **33:** 677—Catagan, Mindanao.
*Draco fimbriatus mindanensis* Hennig, 1936, op. cit., p. 203.

*Diagnosis.* A large species, adults 90–110 mm SV; 5 ribs in patagium; nostrils pointing dorsally; small tympanic scales; usually 4 incisors; 69% with 13 or 14 supralabials; 69% with 7–9 scales bordering rostral; subcaudals more than 2 times length of adjacent scales; dewlap elongate, tapering to narrow tip, covered with small scales.

**Draco obscurus** Boulenger

*Draco obscurus* Boulenger, 1887, Ann. Mag. Nat. Hist., ser. 5, **20:** 95—Mt. Kina Balu, Sabah.
*Draco formosus* Boulenger, 1900, Ann. Mag. Nat. Hist., ser. 7, **6:** 190—Larut Hills, Malaya; Hennig, 1936, op. cit., p. 216.

*Diagnosis.* A moderate-sized species, adults usually less than 95 mm SV; 5 ribs in patagium; nostrils pointing dorsally; 4 incisors; 82% with 9 or 10 supralabials; 63% with 6 scales bordering rostral; subcaudals 1.25–1.5 times length of adjacent scales; dewlap tapering near base then expanding, with rounded tip, covered with very large scales; males from Malay Peninsula with low caudal crest. Two males, both from the Malay Peninsula, exceed the usual size range: 100 and 113 mm.

**Draco quinquefasciatus** Gray

*Draco quinquefasciatus* Gray, 1827, Zool. J., **3:** 219—Penang Island; Hennig, 1936, op. cit., p. 192.

*Diagnosis.* A moderate-sized species, adults 85–110 mm SV; 6 ribs in patagium; nostrils pointing dorsally; small tympanic scales; 4 incisors; 78% with 12–14 supralabials; 65% with 8 or 9 scales bordering rostral; subcaudals 1.3–2 times length of adjacent scales; dewlap elongate, tapering to narrow tip, covered with small scales.

**Draco taeniopterus** Günther

*Draco taeniopterus* Günther, 1861, Proc. Zool. Soc. London, **1861:** 187—Chantaboum, Thailand; Hennig, 1936, op. cit., p. 209.

*Diagnosis.* A small species, adults less than 80 mm SV; 5 ribs in patagium; nostrils pointing dorsally; a large tympanic scale; 4 incisors; 74% with 7 or 8 supralabials; 60% with 7 scales bordering rostral; subcaudals 1.1–1.3 times length of adjacent scales; dewlap tapering near base then expanding, tip broad, covered with large scales.

**Draco volans** Linnaeus

*Draco volans* Linnaeus, 1758, Syst. Nat., 10th ed., p. 199—"India"; Hennig, 1936, op. cit., p. 176.

*Dracunculus spilopterus* Wiegmann, 1834, Nova Acta Acad. Caes. Leopold, **1:** 216—Luzon.
*Draco spilopterus spilopterus* Hennig, 1936, op. cit., p. 185.
*Dracunculus ornatus* Gray, 1845, Cat. Lizards, p. 235—Philippines.
*Draco reticulatus* Günther, 1864, Rep. Br. India, p. 125—Philippines.
*Draco volans reticulatus* Hennig, 1936, op. cit., p. 179.
*Draco cornutus* Günther, 1864, op. cit., p. 125—Borneo.
*Draco spilopterus cornutus* Hennig, 1936, op. cit., p. 183.
*Draco rostratus* Günther, 1864, op. cit., p. 127—"Borneo?".
*Draco guentheri* Boulenger, 1885, Cat. Lizards, **1:** 257—Philippines.
*Draco everetti* Boulenger, 1885, op. cit., p. 258—northeastern Mindanao and Dinagat.
*Draco quadrasi* Boettger, 1893, Kat. Senckenb. Mus., p. 41—Sibuyan.
*Draco rizali* Wandollek, 1900, Abh. Ber. Mus. Dresden, p. 15—Dapitan, Mindanao.
*Draco gracilis* Barbour, 1903, Proc. Biol. Soc. Wash., **16:** 59—Sarawak.

*Diagnosis.* A small species, adults rarely more than 80 mm SV; 6 ribs in patagium; nostrils pointing laterally; tympanic scales variable; 4 or 5 incisors; 64% with 9 or 10 supralabials; 76% with 4–6 scales bordering rostral; subcaudals 0.95–1.15 times length of adjacent scales; dewlap triangular, covered with small scales. See text and Appendix for variation.

The synonymies reflect differences in definition of species between this work and Hennig's (1936). These differences are listed below.

| | |
|---|---|
| *D. lineatus bimaculatus* | *D. bimaculatus* |
| *D. punctatus* | *D. cristatellus* |
| *D. fimbriatus fimbriatus* (part) | *D. cristatellus* |
| *D. fimbriatus mindanensis* | *D. mindanensis* |
| *D. s. spilopterus* | *D. volans* |
| *D. s. cornutus* | *D. volans* |

One additional difference from Hennig's usage is replacement of the name *formosus* Boulenger by *obscurus* Boulenger on grounds of priority.

## INTER- AND INTRASPECIFIC VARIATION

### Recognition of Species' Boundaries

At any given locality, the lizards of the genus *Draco* form distinct morphological clusters, which simplify the recognition of species, even though as many as six species may co-occur. For example, 1,406 individuals collected at Nanga Tekalit, Sarawak (lat. 1°37′ N, long. 113°35′ E) form six well-defined forms based on size, number of ribs in the patagium, orientation of the nostril, scalation and shape of dewlap, color of dewlap, and various quantitative characters (table 1). A plot (fig. 1) of a sampling of males of these forms[2] from Nanga Tekalit according to their scores in the first two axes of a principal components analysis of quantitative characters (see Methods) shows the separation of these clusters except for two, *maximus* and *quinquefasciatus*. These last two closely related forms are easily distinguished from each other by the color pattern of the patagium and the color of the males' dewlaps (table 1).

The clustering of forms at Nanga Tekalit in the principal components analysis can be measured by calculating the euclidean distance between pairs of individuals with respect to their scores in the first three axes, which account for 66% of the

[2]Excluding *haematopogon*, only one of which was caught at Nanga Tekalit.

TABLE 1. Characteristics of species of *Draco* that co-occur at Nanga Tekalit, Sarawak.

| Character | *volans* | *melanopogon* | *haematopogon* | *obscurus* | *maximus* | *quinquefasciatus* |
|---|---|---|---|---|---|---|
| No. of ribs | 6 | 5 | 5 | 5 | 6 | 6 |
| Nostril orientation | lateral | dorsal | dorsal | dorsal | dorsal | dorsal |
| Tympanic scale | large | large | large | large | small | small |
| Prefrontal keeled ridge | inverted Y | absent | absent | linear | linear, weak | absent |
| Dewlap shape (♂) | triangular, short | elongate, not tapering in distal third | triangular, elongate | clavate | elongate, tip pointed | elongate, tapering in distal third |
| Dewlap scales (♂) | small | small | large near tip | very large | small | small |
| Color of dewlap (♂) | orange or yellow | jet black | red basally, yellowish green distally | grayish brown | pale brown or gray | yellow |
| Color of neck flaps ventrally (♂) | bright yellow with black spots | jet black | deep red | dull red | purple-black with white spots | bright yellow |
| Pattern of wing dorsally | dark gray with obscure black bands | dark with small light spots | dark with small light spots | transverse bands | dark with short light lines | transverse bands |
| Dewlap (♀) | absent | small tag | absent | small tag | small tag | small tag |
| S-V ♂ range | 73–77 | 69–85 | 66–75 | 80–87 | 126–139 | 86–100 |
| Supralabials (modal value) | 7–10 (8) | 11–14 (12) | 10–13 (12) | 7–11 (9) | 12–15 (14) | 11–14 (12) |
| Scales around rostral (modal value) | 4–8 (5) | 6–12 (9) | 6–9 (8) | 5–7 (6) | 8–12 (9) | 6–12 (9) |

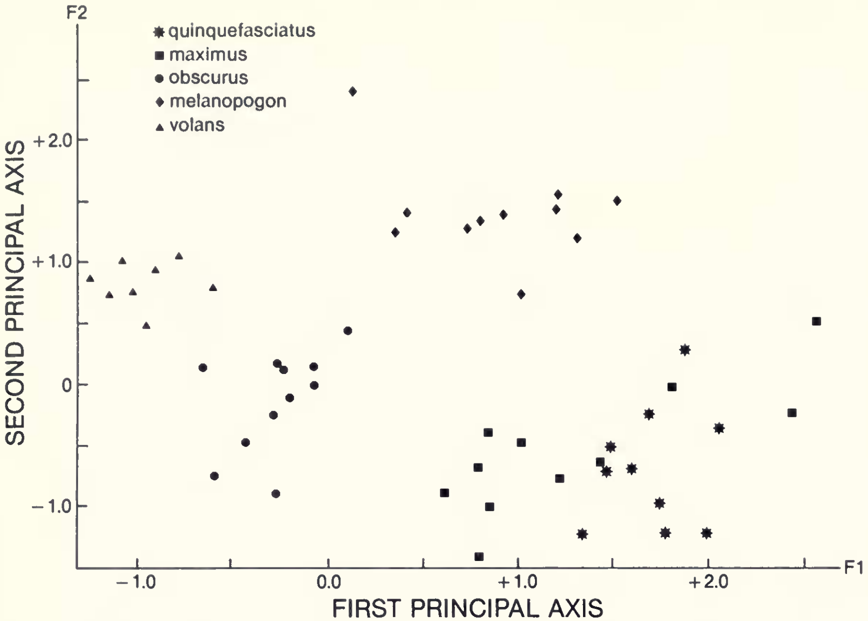


FIG. 1. Males of five co-occurring species of *Draco* plotted on the first two axes of a principal components analysis. All lizards collected at Nanga Tekalit, Sarawak.

TABLE 2. Mean distances of scores in first three principal components axes within and between species of *Draco* occurring at Nanga Tekalit, Sarawak (number of distances calculated in parentheses; males only used in principal components analysis).

| | *volans* | *melanopogon* | *obscurus* | *maximus* | *quinquefasciatus* |
|---|---|---|---|---|---|
| *volans* | 0.77 ± .02 (351) | 2.57 ± .02 (270) | 2.36 ± .03 (297) | 3.22 ± .01 (756) | 2.74 ± .03 (297) |
| *melanopogon* | | 0.92 ± .01 (1,275) | 2.19 ± .05 (110) | 2.70 ± .04 (280) | 2.37 ± .05 (110) |
| *obscurus* | | | 0.69 ± .02 (231) | 3.07 ± .03 (308) | 2.37 ± .06 (121) |
| *maximus* | | | | 0.97 ± .02 (378) | 1.28 ± .03 (308) |
| *quinquefasciatus* | | | | | 0.89 ± .01 (990) |
| | **Sample sizes used in calculating distances** | | | | |
| Interspecific distances | 27 | 10 | 11 | 28 | 11 |
| Intraspecific distances | 27 | 51 | 22 | 28 | 45 |

| | **Sources of samples** | |
|---|---|---|
| **Species** | **Within species** | **Between species** |
| *volans* | Sarawak | Sarawak |
| *melanopogon* | entire range | Nanga Tekalit, Sarawak |
| *obscurus* | entire range | Sarawak |
| *maximus* | entire range | entire range |
| *quinquefasciatus* | entire range | Nanga Tekalit, Sarawak |

total variation. The mean distance for interspecific pairs of individuals is significantly larger (at $P < .01$ level, $t$ tests) than the corresponding intraspecific means for every pair of species (table 2). The intraspecific means were based on larger geographic samples, which is a conservative bias, as this procedure should increase mean distance. The results in Table 2 clearly show that, even for such similar forms as *quinquefasciatus* and *maximus*, at a given locality, the individuals of each species form a cluster well separated from those of other species.

With the exception of *haematopogon*, the same distinct morphological types appeared in two samples from the state of Selangor, West Malaysia (at Ulu Gombak and Bukit Lanjan). Agreement between West Malaysian and Sarawak samples of corresponding forms in qualitative characters is very close. Slight but statistically significant ($P < .05$) geographic variation appears in some quantitative characters (table 3). However, these differences within forms do not blur the larger differences between forms. For example, both *volans* and *melanopogon* show statistically significant geographic variation in the number of scales touching the rostral ($P < .05$, $t$ tests), yet the gap between the two forms in this character remains relatively large (table 3).

Another view of the distinctiveness of species of *Draco* from one another can be obtained from the principal components analysis (see Methods), in which the position of each species is plotted with respect to the first three components (fig. 2). The species are generally well separated except for *obscurus* (8 in fig. 2), *taeniopterus* (9), and *blanfordi* (10), which are very similar and are discussed below.

Because of the consistent gaps between forms and the slight amount of geographic variation, it is relatively easy to assign names from the literature to most of the morphological types in this genus, as has been done in Tables 1–3. In some cases intraspecific variation, local or geographic or both, complicates the task of species recognition. For example, slight geographic variation in coloration of the dewlap and neck lappets in the species called *D. obscurus* Boulenger in this paper led Boulenger (1887, 1900) to describe Malayan and Bornean samples as separate species. This species is quite similar to *D. taeniopterus* Günther. As the ranges of these two overlap in the central part of the Malay Peninsula, there is some possibility for confusion although, as shown below, all individuals can be definitely assigned to one or the other species. A third species, *D. blanfordi* Boulenger, similar to the preceding ones in having large scales on the dewlap, is sexually dimorphic in the dorsal pattern of the patagium, the female having a pattern similar to those of both sexes of *obscurus* and *taeniopterus*. *Draco cristatellus* Günther and *D. fimbriatus* Kuhl, alike in many qualitative characters and with overlapping ranges of variation in a number of quantitative ones, are even more difficult to separate than the preceding set of species. The most important example, however, of confusing patterns of variation involves the populations grouped under the names *volans* and *spilopterus* by Hennig (1936). These cases will be discussed in turn below.

For the rest, the characteristics given in the diagnoses suffice for species recognition. Occasionally, coloration of the patagium or dewlap may be needed. Omitting *volans* (and the nominate forms implied in its synonymy, p. 8), three species have six ribs supporting the patagium: *maximus*, *quinquefasciatus*, and *dussumieri*. The last is distinguished from the first two by the large tympanic scale. *Draco maximus* is much larger than *quinquefasciatus* (see Appendix), and the two differ sharply in coloration of the patagium and dewlap (table 1).

The remaining species, with five ribs in the patagium, include five with the

Table 3. Geographic variation in selected characters of *Draco* species that co-occur in both Borneo and the Malay Peninsula. Definitions of characters given in Materials and Methods.

| Character | *volans* | | *melanopogon* | | *obscurus* | | *maximus* | | *quinquefasciatus* | |
|---|---|---|---|---|---|---|---|---|---|---|
| | Borneo | Malaya | Borneo | Malaya | Borneo | Malaya | Borneo | Malaya | Borneo | Malaya |
| Snout-vent (♂) | | | | | | | | | | |
| N | 39 | 17 | 35 | 20 | 17 | 14 | 23 | 6 | 32 | 13 |
| Range | 66–82 | 66–76 | 69–85 | 69–83 | 71–91 | 75–113.5 | 117–137 | 129–138 | 82–100 | 92–110 |
| Mean ± SE | 71.8 ± .62 | 71.0 ± .66 | 77.8 ± .52 | 75.2 ± .61 | 82.6 ± .95 | 87.2 ± 2.65 | 130.7 ± 1.07 | 132.2 ± 1.35 | 89.8 ± .75 | 96.8 ± 1.39 |
| Supralabials | | | | | | | | | | |
| N | 67 | 23 | 36 | 35 | 20 | 18 | 35 | 8 | 37 | 17 |
| Range | 7–11 | 7–11 | 10–15 | 10–15 | 7–11 | 7–11 | 12–18 | 13–15 | 10–17 | 11–15 |
| Mean ± SE | 8.9 ± .10 | 8.8 ± .18 | 11.9 ± .17 | 12.5 ± .18 | 9.2 ± .20 | 9.3 ± .21 | 14.6 ± .24 | 14.5 ± .27 | 12.7 ± .21 | 13.5 ± .29 |
| Scales around rostral | | | | | | | | | | |
| N | 62 | 15 | 36 | 22 | 8 | 11 | 29 | 7 | 35 | 17 |
| Range | 4–6 | 5–8 | 6–12 | 8–12 | 5–7 | 5–7 | 8–12 | 9–11 | 6–13 | 7–11 |
| Mean ± SE | 5.2 ± .13 | 6.7 ± .25 | 8.9 ± .20 | 9.8 ± .21 | 6.0 ± .19 | 5.7 ± .19 | 9.4 ± .21 | 10.0 ± .31 | 8.7 ± .24 | 8.8 ± .21 |
| Incisors | | | | | | | | | | |
| N | 56 | 19 | 32 | 27 | 11 | 9 | 29 | 5 | 32 | 13 |
| Range | 4–6 | 3–5 | 4 | 4 | 4 | 4 | 4–6 | 3–4 | 4 | 4 |
| Mean ± SE | 5.0 ± .04 | 4.8 ± .12 | 4.0 | 4.0 | 4.0 | 4.0 | 4.5 ± .12 | 3.8 | 4.0 | 4.0 |
| Tympanic scale | | | | | | | | | | |
| N | 41 | 14 | 31 | 18 | 14 | 11 | 26 | 6 | 31 | 13 |
| Range | .18–1.50 | .38–1.15 | 1.00–1.67 | .92–1.62 | .30–.94 | .65–1.00 | .11–.43 | .10–.30 | .13–.33 | .18–.40 |
| Mean ± SE | .88 ± .03 | .88 ± .08 | 1.32 ± .03 | 1.29 ± .06 | .67 ± .05 | .87 ± .04 | .22 ± .02 | .20 ± .03 | .19 ± .01 | .28 ± .02 |
| Dewlap length (♂) | | | | | | | | | | |
| N | 38 | 14 | 36 | 24 | 16 | 10 | 22 | 6 | 31 | 13 |
| Range | .27–.34 | .32–.37 | .36–.45 | .40–.49 | .34–.40 | .38–.46 | .39–.47 | .42–.45 | .39–.50 | .37–.50 |
| Mean ± SE | .31 ± .003 | .34 ± .004 | .41 ± .005 | .44 ± .005 | .38 ± .004 | .41 ± .007 | .43 ± .004 | .44 ± .005 | .45 ± .005 | .45 ± .009 |
| Caudals | | | | | | | | | | |
| N | 53 | 14 | 27 | 18 | 13 | 11 | 24 | 5 | 31 | 13 |
| Range | .79–1.12 | .78–1.03 | .45–.76 | .55–.90 | .50–.94 | .63–.82 | .49–.75 | .45–.70 | .45–.81 | .45–.65 |
| Mean ± SE | .99 ± .009 | .95 ± .019 | .61 ± .024 | .68 ± .024 | .72 ± .029 | .73 ± .018 | .60 ± .014 | .52 | .58 ± .020 | .53 ± .006 |

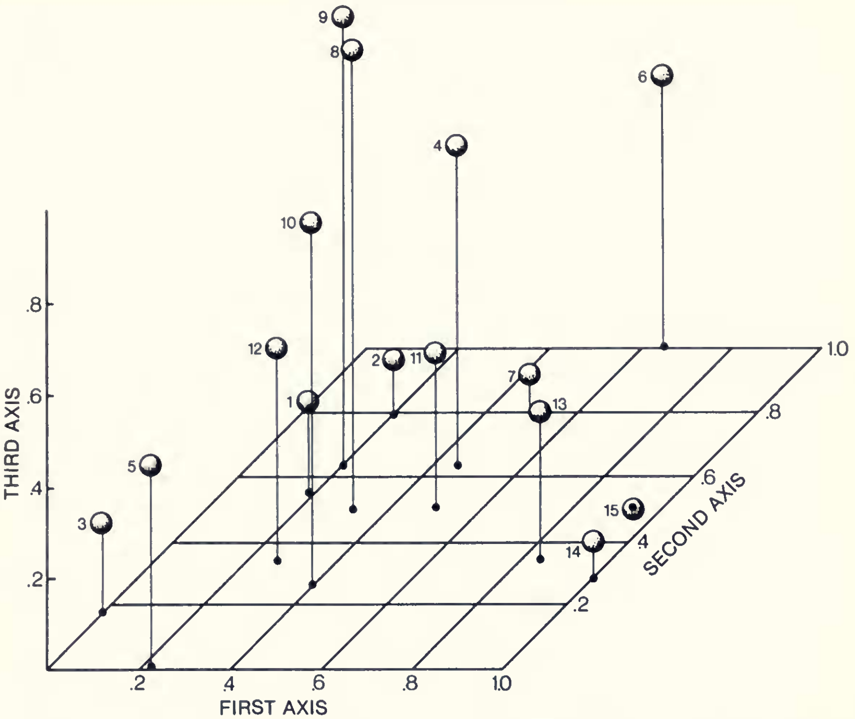


FIG. 2. Males of *Draco* species plotted by mean intraspecific scores on three principal component axes. Plot on each axis standardized by: $(\overline{X}_i - \overline{X}_{min}) / (\overline{X}_{max} - \overline{X}_{min})$, where $\overline{X}_i$ equals mean of species i and $\overline{X}_{min}$ and $\overline{X}_{max}$ equal, respectively, minimum and maximum species means on given axis. Species are numbered on the plot as: *bimaculatus* (2), *blanfordi* (10), *cristatellus* (12), *dussumieri* (4), *fimbriatus* (11), *haematopogon* (7), *lineatus* (3), *maculatus* (5), *maximus* (14), *melanopogon* (6), *mindanensis* (15), *obscurus* (8), *quinquefasciatus* (13), *taeniopterus* (9), and *volans* (1).

nostrils pointing laterally: *fimbriatus, cristatellus, bimaculatus, maculatus,* and *lineatus*. The first three have large tympanic scales, and the others, small ones. *Draco bimaculatus* and *lineatus* have five incisors, *cristatellus* four or five, and the others four. Males of *cristatellus* differ from those of *bimaculatus* and *lineatus* in having a low caudal crest. In some individuals of *fimbriatus* and *cristatellus,* the axis of the nostril is oblique as in *blanfordi,* but the last differs from the other two in having distinctly enlarged scales on the dewlap. The rest of the species with five ribs in the patagium have the nostril pointing dorsally. One of them, *mindanensis,* is distinguished by the small scales covering the tympanum. *Draco melanopogon* is the only species having a jet black dewlap. *Draco haematopogon* and *melanopogon* have more supralabials (respectively, 78% with 11 or 12 and 84% with 11 to 13) than *obscurus* and *taeniopterus* (more than 90% of each with 10 or fewer). These last two have clearly defined transverse bands dorsally on the patagium and distinctly enlarged scales on the dewlap.

### **Draco obscurus** vs. **D. taeniopterus** and **D. blanfordi**

The ranges of *obscurus* and *taeniopterus* overlap in extreme southern peninsular Thailand. Both species have five ribs supporting the patagium, nostrils oriented dorsally, relatively large tympanic scale, and, in males, the dewlap not tapering and even widening slightly in its distal half and covered with very large scales. However, the dewlap is distinctly wider and its scales larger in males of *obscurus* (table 4); the largest dewlap scales are conspicuously larger than the nasal scale in males of *obscurus* but at most only slightly larger than the nasal in male *taeniopterus*. Females of both species have a distinct gular appendage; in *taeniopterus* it is small (about the size of the nasal scale) and covered with small scales equal to those of the adjacent throat, whereas in *obscurus* it is much larger than the nasal and is covered with distinctly enlarged scales several times the size of those on the throat. The two species also differ in average snout-vent length, number of supralabials, number of scales touching the rostral, dewlap length, and relative size of the tympanic scale (table 4).[3] Smith (1937) noted that the dark transverse bands on the dorsal surface of the patagium are more conspicuous and well defined in *taeniopterus*. Although this distinction is real, it is not easy to see in all preserved material.

---

[3]Differences noted are significant at the $P < .05$ level. *T* tests were carried out on snout-vent and meristic characters, and Mann-Whitney U tests, on the others.

TABLE 4. Comparison of *Draco obscurus* Boulenger (samples from Malay Peninsula), *D. taeniopterus* Günther, and *D. blanfordi* Boulenger.

| **Character** | *obscurus* | *taeniopterus* | *blanfordi* |
|---|---|---|---|
| Snout-vent (♂) | | | |
| Range (N) | 75–113.5 (14) | 66.5–80 (22) | 102–131 (18) |
| Mean ± SE | 87.2 ± 2.65 | 73.8 ± 0.86 | 119.1 ± 1.81 |
| Supralabials | | | |
| Range (N) | 9–11 (18) | 7–10 (35) | 7–11 (28) |
| Mean ± SE | 9.3 ± .21 | 8.2 ± .15 | 9.1 ± .17 |
| Scales around rostral | | | |
| Range (N) | 5–7 (11) | 5–7 (10) | 5–9 (29) |
| Mean ± SE | 5.7 ± .19 | 6.5 ± .22 | 7.3 ± .17 |
| Lamellae fourth toe | | | |
| Range (N) | 20–28 (10) | 23–28 (14) | 25–36 (9) |
| Mean ± SE | 24.2 ± .65 | 24.5 ± .44 | 28.0 ± .11 |
| Dewlap length (♂)* | | | |
| Range (N) | .38–.46 (10) | .39–.46 (16) | .38–.45 (16) |
| Mean ± SE | .41 ± .007 | .43 ± .005 | .42 ± .005 |
| Dewlap width (♂)* | | | |
| Range (N) | .050–.095 (12) | .038–.058 (10) | .049–.078 (12) |
| Mean ± SE | .065 ± .004 | 0.47 ± .002 | .062 ± .003 |
| Largest dewlap scale* | | | |
| Range (N) | .021–.030 (11) | .015–.020 (8) | .013–.019 (17) |
| Mean ± SE | .025 ± .001 | .017 ± .001 | .016 ± .001 |
| Tympanic scale** | | | |
| Range (N) | .65–1.00 (11) | .65–1.25 (10) | .28–1.17 (21) |
| Mean ± SE | .87 ± .04 | 1.05 ± .08 | .77 ± .05 |

*Relative to snout-vent. **Relative to nasal scale.

The range of *D. blanfordi* overlaps the southern part of that of *taeniopterus* and the northern part of the range of *obscurus*. Like those two species, males of *blanfordi* have a dewlap widening near its center and covered by large scales. Females, but not males, of *blanfordi* have dark transverse bars dorsally on the patagium generally similar to those of the other two species. However, unlike *obscurus* and *taeniopterus* in which the nostrils point dorsally, in *blanfordi* the nostrils are oriented dorsolaterally (noted by Hennig, 1936), and the projection of the narial axis falls on the canthal line when the animal is viewed head-on. *Draco blanfordi* is also much larger than the other two species and has more scales around the rostral and more lamellae under the fourth toe (table 4). Females of *blanfordi* have gular appendages much like those of females of *obscurus* in length and size of scales and are, therefore, different from those of females of *taeniopterus* in these regards. *Draco blanfordi* also differs statistically from *obscurus* in the length of the dewlap and size of its scales (in males) and from *taeniopterus* in number of supralabials and size of the tympanic scale (table 4).[4]

### Draco fimbriatus vs. D. cristatellus

Unlike the preceding set of three species, all individuals of *fimbriatus* and *cristatellus* are not easily assigned to one or the other species. Grandison (1972), reporting on one male of each species from Gunong Benom, West Malaysia, noted that in *fimbriatus* the dewlap and the underside of the neck lappets were coral pink, whereas these surfaces were bright yellow in *cristatellus* (as *punctatus*). Unfortunately, this distinction, which must be important in the lives of these species, is not evident in preserved specimens. With samples of each species at hand, a suite of statistical differences emerges.

The specimens examined which agree with descriptions of *fimbriatus* and *cristatellus* fall into two distinct size groups (table 5), the smaller embracing the types of *cristatellus* and its synonym *punctatus*. All the males included in the table are apparently mature, having fully developed dewlaps and caudal crests. The largest and smallest females of *cristatellus* are gravid; the smallest gravid *fimbriatus* measures 102 mm. Accepting these size-defined forms, the two species are found to differ statistically in a number of characters, although their ranges of variation overlap (table 5). They do not differ in the size of subcaudals relative to adjacent rows. Five individuals of *cristatellus*, but none of *fimbriatus*, examined had five incisors. All of the *cristatellus* individuals seen had small blackish spots on the dorsal surfaces of head and trunk. Similar spotting, though not as dense, occurred in nine *fimbriatus* males. The remaining *fimbriatus* of both sexes (N = 29) had a barklike pattern dorsally (see description in Grandison, 1972).

### Draco volans Group

Recognition of species boundaries and application of names from the literature are most difficult when dealing with the forms or populations grouped by Hennig (1936) under the names *volans* and *spilopterus*. These populations, considered as a group, range from peninsular Thailand through the Greater and Lesser Sundas as

---

[4]Statistical differences mentioned in this paragraph are significant at the $P < .05$ level. *T* tests were used for snout-vent and meristic characters, and Mann-Whitney U tests, for the other characters.

TABLE 5. Statistically significant differences between samples of *Draco cristatellus* and *fimbriatus*.

| Character | Sex | *fimbriatus* N | *fimbriatus* Range | *fimbriatus* Mean / median* | *cristatellus* N | *cristatellus* Range | *cristatellus* Mean / median* | P** |
|---|---|---|---|---|---|---|---|---|
| SIZE AND SCALE COUNTS | | | | | | | | |
| Snout-vent (mm) | ♂ | 24 | 97–132 | 108.0 ± 1.53 | 10 | 70–90 | 83.2 ± 2.01 | .001 |
| Snout-vent (mm) | ♀ | 16 | 95–119 | 105.9 ± .55 | 3 | 79–88 | 82.4 | |
| Supralabials | ♂ + ♀ | 44 | 9–14 | 11.6 ± .17 | 12 | 9–12 | 10.1 ± .26 | .01 |
| Scales around rostral | ♂ + ♀ | 42 | 4–10 | 7.1 ± .21 | 11 | 5–7 | 6.4 ± .28 | .05 |
| Lamellae, 4th toe | ♂ + ♀ | 23 | 23–28 | 25.4 ± .33 | 9 | 22–25 | 23.9 ± .31 | .02 |
| BODY AND SCALE PROPORTIONS | | | | | | | | |
| Dewlap length | ♂ | 24 | .359– .458 | .428 | 8 | .330– .417 | .358 | .002 |
| Snout length | ♂ + ♀ | 29 | .374– .479 | .403 | 11 | .362– .423 | .383 | .01 |
| Tympanic scale | ♂ + ♀ | 26 | .954–1.690 | 1.238 | 11 | .765–1.267 | 1.063 | .003 |

*Mean ± standard error given for snout-vent and scale counts; median for proportional characters.

**For snout-vent and scale counts, *t* test applied to interspecific comparisons; for other characters, Mann-Whitney test was used. Definitions of proportions given in Materials and Methods.

far east as Timor and Ceram and northward through the Philippines to Luzon. Their combined geographic range, therefore, almost equals the range of the entire genus. As in addition they account for the largest array of nominate forms in the genus, resolution of a number of taxonomic and biological questions depends upon understanding the patterns of variation of the *volans* group. In the discussion that follows, I omit consideration of the populations from the Lesser Sundas, as they are currently being studied by Musters.

The characters shared by all these populations include: six ribs supporting the patagium, nostrils pointed laterally, males without a caudal crest, dewlap in males covered with small scales and tapering continuously from its base. However, these populations exhibit unusual variation in coloration, locally as well as geographically, in pattern of carination and size of head scales, and in various quantitative characters. The two most important features of variation within this group are (1) the involvement of almost all characters examined and (2) the lack of concordance among characters. We will consider these two features in sequence. We will also deal with (3) the comparison of overall variation in the *volans* group with that in other species, because such comparisons inevitably affect taxonomic decisions.

*Feature 1.* —The range of coloration of the patagium is extensive. In preservative the dorsal surface may be dark brown or blackish without evident pattern, light with small dark spots laterally or over the entire surface, or marked with large black spots or transverse bands enclosing light areas. A large orange, blue, or black area may be superimposed laterally on these patterns. The colors in life of this surface have been recorded in males as: West Malaysia—proximally bronze-brown, orange red in the center, and dark distally with dark spots across the entire surface (Flower, 1896) and brown with dark gray transverse bands (Grandison, 1972); Borneo—black transverse bands with ground color pea green proximally, becoming dark gray laterally (FMNH 138417); Mindanao—dark "with numerous roundish spots of bluish to yellowish green, the outer edge light salmon" or brownish with "five large elongate blotches of yellowish green between the ribs (ultramarine in alcohol)" (Taylor, 1922). Females have been recorded as: West Malaysia—as in the male, except rich yellow replaces the red ground color (Flower, 1896), and brown with gray transverse bands as in the male (Grandison, 1972); Borneo—gray with brown transverse bands proximally, deep red in center, and black with white flecks in distal quarter (FMNH 150609); Mindanao—black washed with gray, enclosing bright reddish to orange spots that are lighter near the body, and dark with large blotches of blue in proximal third (Taylor, 1922). Descriptions of color in life of more individuals and from other parts of the range would undoubtedly expand the variation.

Preserved material shows both geographic and local variation (tables 6–7). In Borneo, for example, although the dorsal surface of the patagium is generally dark, some individuals of both sexes have a distinct transverse pattern, and about one-fourth have large yellow or orange areas. Light dorsal pigmentation prevails in males from Samar, Negros, and the northern Philippines, in contrast to those from Mindanao, Borneo, and the continent (table 6). Females do not show comparable geographic dichotomy.

Although the ventral surface of the patagium has light coloration in all individuals, the amount and position of black spotting varies (table 7). The widest ranges of regional variation are shown by males from Mindanao and females from Borneo. Among males a sharp dichotomy exists between, on the one hand, the

TABLE 6. Dorsal coloration of patagium in preserved specimens of the *Draco volans* group.

| | General pattern | | | Superimposed coloration† | | | |
|---|---|---|---|---|---|---|---|
| Population | Dark, no pattern | Dark*-dominant | Light**-dominant | None | Orange or yellow area distally | Blue areas in center | Large black area distally |
| *Males:* | | | | | | | |
| Thailand | | 4 | | 4 | | | |
| Malaya | | 17 | | 15 | | | 2 |
| Borneo | 23 | 9 | | 25 | 7 | | |
| Mindanao | 4 | 19 | | 6 | | 16 | 1 |
| Negros | | | 18 | 18 | | | |
| Samar | | 2 | 10 | | | | 12 |
| Cebu | | | 9 | 9 | | | |
| N. Philippines‡ | | | 17 | 17 | | | |
| *Females:* | | | | | | | |
| Thailand | 1 | 5 | | 6 | | | |
| Malaya | 6 | 5 | | 11 | | | |
| Borneo | 10 | 9 | 1 | 17 | 3 | | |
| Mindanao | 2 | 2 | | 2 | | 1 | 1 |
| Negros | 9 | 1 | | 10 | | | |
| Samar | | 7 | | | | | 7 |
| Cebu | 3 | 6 | | 9 | | | |
| N. Philippines‡ | 4 | 3 | | 7 | | | |

*Patagium surface predominantly dark brown or black with a transverse pattern. **Patagium surface mainly light with dark pigment in form of small spots varying in position, number, and arrangement.

†Large blotches of pigment superimposed on pattern. ‡Combined samples from Luzon, Lubang, Sibuyan, and Marinduque.

TABLE 7. Ventral coloration of patagium in preserved specimens of *Draco volans* group, all with light ground color.

| Population | Immaculate | Short black band or spots at lateral margin | Black spots in anterodistal quadrant | Entire surface spotted |
|---|---|---|---|---|
| *Males:* | | | | |
| Thailand | | | | 3 |
| Malaya | | | | 18 |
| Borneo | | 2 | | 31 |
| Mindanao | 3 | 8 | 12 | 1 |
| Negros | 5 | 11 | | |
| Samar | | | 12 | |
| Cebu | 1 | | 8 | |
| N. Philippines* | 1 | 8 | | 1 |
| *Females:* | | | | |
| Thailand | | | | 7 |
| Malaya | | | 1 | 10 |
| Borneo | 1 | 4 | 1 | 14 |
| Mindanao | | 3 | 3 | |
| Negros | | 6 | 4 | |
| Samar | | 5 | 12 | |
| Cebu | | 5 | 4 | |
| N. Philippines* | | 2 | 1 | 1 |

*Combined samples from Lubang, Sibuyan, and Marinduque.

continental and Bornean samples, which have the entire ventral surface spotted, and, on the other, the Philippine samples, in which spotting is restricted. Females show approximately the same geographic separation, though Bornean individuals blur the demarcation. Within the Philippine sample, males from Negros and the Northern Philippines have less black pigment than those from Cebu and Samar; males from Mindanao overlap both of these groups. Females, however, do not show interisland differences within the Philippines.

The coloration of the male dewlap also varies. In life the dewlap is orange to bright yellow in males from West Malaysia (Flower, 1896; Grandison, 1972) and Borneo; blue basally, yellow to flesh color distally in males from peninsular Thailand (Taylor, 1963); wine to purple-brown basally, yellow to orange distally in males from Mindanao (Taylor, 1922). Males of most populations have the base of dewlap spotted or reticulated with brown. Many males from Borneo, however, lack that dark pattern. The ventral surface of the lateral neck lappets is also brightly pigmented. In one male from Borneo (FMNH 158769), these surfaces were bright chrome yellow with dark spots, and in a second (FMNH 138417), emerald green with spots of pea green to chrome yellow. A male from West Malaysia was grayish (Grandison, 1972).

Carination and elevation of certain scales also are subject to variation in the *volans* group. Populations on the continent and the Greater Sundas have large keeled scales on the snout and forehead arranged as an inverted Y, with the arms ending in the supraocular region. The same arrangement appears in the southern Philippine Islands, Jolo, Mindanao, and Palawan. In the rest of the Philippines (Negros and Samar northward), usually only the stem of the Y on the snout is present; in some individuals from this area, the lateral arms are represented by weakly keeled scales in which the keels do not form a continuous line, but instead the keel of each scale is parallel to the stem of the Y.

Almost all individuals of this group have a sharp, hard, inflexible cone at the end of the supraciliary line. Slightly in advance of this cone and separated from it is an enlarged scale. In most individuals of both sexes from Borneo, Mindanao, and Jolo, this scale is taller than its anteroposterior axis and clearly flexible. In all other populations, the height of this supraciliary "horn" is usually less than its length; in most individuals of these populations, it is not flexible.

Males of most species of *Draco* can raise a ridge on the neck (see photograph in Hairston, 1957), presumably by muscular contractions, but few have specialized nuchal crest scales, i.e., scales distinguished by shape and size from adjacent ones. Males in most populations in the *volans* group, however, have distinct nuchal crest scales that are laterally compressed and rise above adjacent scales by a height equal to their anteroposterior length. The number of these scales varies greatly (table 8). In males from West Malaysia, for example, the number varies from 4 to 15, in those from Mindanao, 0 to 20, and in those from Negros, 0 to 6. Males from Borneo exhibit a clearly bimodal distribution, one group having 0 to 4, and the other, 9 to 16.

Statistically significant variation among these populations is evident in relative sizes of certain scales, in relative length of the dewlap, and in meristic characters (table 8). Snout-vent does not vary significantly, and even though the means appear to differ between some pairs of populations, all of the large samples (ca. $> 10$) have approximately the same range (males ca. 63–78 mm).

*Feature 2.* —The lack of concordance of variation among characters was alluded to above in the description of variation in color pattern. A major break in dorsal pattern of the patagium in males occurs between Mindanao and the Philippine Islands to the north. In terms of ventral pattern in males, the major break lies between Borneo and Mindanao. The flexible supraciliary "horn" separates the populations of Borneo (but see below), Jolo, and Mindanao from the remainder. The dividing line between populations characterized by small scales covering the tympanum and those having large tympanic scales falls between Palawan, Mindanao, and Cebu on one side and the remainder of the Philippines on the other (table 8). High counts of nuchal crest scales are found in Mindanao and southward and westward, except for a pocket in Palawan and Borneo (but see below). High counts of supralabials (i.e., mean $> 9.5$) occur in a band across Palawan, Jolo, and Mindanao and then again north of Samar and Sibuyan (table 8). Populations having four "incisors" as the modal value lie north of Negros and Cebu, except for the Sibuyan population (modal value 5) and, to the south, the sample from Jolo (modal value 4).

The populations in the Philippines lying north of Mindanao share several character states, such as light patagia in males (table 7), incomplete keeled Y on top of the snout, and, except for the Cebu population, small scales covering the tympanum (table 8). As the last character has been used to define one of the nominate forms, *spilopterus* (Wiegmann), in the *volans* species group, the sharing of these three states may confirm the existence of a distinct species or subspecies. However, this subgroup of populations is internally heterogeneous in a complex way. Student-Newman-Keuls analysis (Sokal & Rohlf, 1969) of supralabials, incisors, and scales bordering the rostral based on the data in Table 8 shows the shifting pattern of interpopulational similarities. In terms of supralabials, the Marinduque

TABLE 8. Variation among populations of the *Draco volans* group (except where indicated, both sexes included; definitions of characters in Materials and Methods).

| Population | Snout-vent (♂) | | Supralabials | | Scales around rostral | | Incisors | | Nuchal crest scales (♂) | | Tympanic scale | | Dewlap length (♂) | | Caudals | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | N | Mean ± SE | N | Mean ± SE | N | Mean ± SE | N | Mean ± SE | N | Mean ± SE | N | Mean ± SE | N | Mean ± SE | N | Mean ± SE |
| Thailand | 10 | 69.4 ± .93 | 15 | 9.1 ± .17 | 13 | 6.5 ± .24 | 13 | 4.8 ± .01 | 10 | 11.6 ± .65 | 11 | .86 ± .06 | 8 | .34 ± .004 | ... | ... |
| Malaya | 17 | 71.0 ± .66 | 25 | 9.0 ± .17 | 20 | 6.7 ± .22 | 26 | 4.8 ± .11 | 17 | 10.4 ± .73 | 18 | .90 ± .06 | 14 | .34 ± .004 | 18 | .96 ± .02 |
| Borneo | 39 | 71.8 ± .62 | 67 | 8.9 ± .10 | 62 | 5.2 ± .13 | 56 | 5.0 ± .04 | 47 | 4.6 ± .74 | 41 | .88 ± .03 | 38 | .31 ± .003 | 53 | .99 ± .01 |
| Sumatra | 5 | 73.8 ± 1.17 | 7 | 8.6 ± .48 | 5 | 6.6 ± .51 | 6 | 5.0 ± 0 | 5 | 12.8 ± .73 | 7 | .82 ± .12 | 5 | .33 ± .010 | ... | ... |
| Java | 12 | 68.8 ± 1.55 | 22 | 8.9 ± .20 | 19 | 5.4 ± .23 | 16 | 4.8 ± .11 | 15 | 9.3 ± .35 | 18 | 1.17 ± .05 | 12 | .32 ± .005 | 13 | .96 ± .03 |
| Palawan | 4 | 75.5 | 8 | 9.9 ± .35 | 8 | 5.4 ± .38 | 7 | 4.7 ± .18 | 6 | 2.0 ± 1.03 | 7 | 1.34 ± .04 | 5 | .33 ± .010 | 5 | .99 ± .01 |
| Jolo | 3 | 76.0 | 7 | 9.9 ± .40 | 7 | 5.7 ± .18 | 5 | 4.2 ± .37 | 3 | 8.0 | 7 | 1.45 ± .11 | 3 | .33 | 6 | .99 ± .03 |
| Mindanao | 22 | 72.7 ± 1.08 | 30 | 10.1 ± .19 | 28 | 5.9 ± .14 | 26 | 4.7 ± .09 | 21 | 11.5 ± 1.42 | 18 | 1.50 ± .04 | 14 | .36 ± .007 | 17 | 1.02 ± .01 |
| Negros | 15 | 73.0 ± 1.30 | 25 | 10.0 ± .20 | 22 | 3.7 ± .19 | 18 | 4.8 ± .19 | 9 | 1.4 ± .69 | 15 | .39 ± .03 | 17 | .41 ± .006 | 14 | 1.00 ± .02 |
| Cebu | 7 | 72.1 ± 1.63 | 16 | 9.6 ± .22 | 16 | 4.0 ± .26 | 8 | 4.8 ± .16 | 8 | 5.1 ± 1.53 | 7 | 1.01 ± .09 | 7 | .38 ± .005 | 7 | .91 ± .05 |
| Samar | 9 | 69.2 ± .92 | 12 | 9.1 ± .29 | 15 | 5.0 ± .20 | 14 | 4.2 ± .11 | 10 | 12.1 ± 1.33 | 12 | .22 ± .01 | 9 | .37 ± .004 | 12 | .97 ± .02 |
| Sibuyan | 8 | 70.8 ± 1.45 | 13 | 9.2 ± .22 | 12 | 5.6 ± .26 | 12 | 4.8 ± .13 | 7 | 3.9 ± 1.78 | 13 | .45 ± .05 | 8 | .39 ± .004 | ... | ... |
| Marinduque | 10 | 72.2 ± 1.00 | 15 | 10.7 ± .25 | 15 | 4.8 ± .28 | 13 | 4.2 ± .10 | 9 | 1.9 ± .81 | 13 | .38 ± .03 | 10 | .40 ± .007 | 10 | .86 ± .04 |
| Lubang | 9 | 70.4 ± 1.57 | 15 | 9.7 ± .25 | 15 | 4.1 ± .24 | 12 | 4.1 ± .08 | 9 | 3.3 ± 1.40 | 15 | .61 ± .06 | 9 | .49 ± .016 | ... | ... |
| Luzon | 7 | 75.0 ± .56 | 11 | 9.8 ± .26 | 11 | 4.6 ± .28 | 7 | 4.0 ± 0 | 5 | 4.4 ± 1.72 | 9 | .43 ± .05 | 7 | .42 ± .009 | 5 | .94 ± .05 |
| ANOVA* results | | *P* > .10 | | *P* < .001 | | *P* < .001 | | *P* < .001 | | *P* < .001 | | *P* < .001 | | *P* < .001 | | *P* < .001 |

*F ratio used for first five characters; Kruskal-Wallis ANOVA used for last three.

and Negros populations are differentiated from the Samar, Sibuyan, and Cebu populations, and the Marinduque also from the Luzon and Lubang. In terms of incisors, the Sibuyan, Cebu, and Negros populations are differentiated from the other four. In terms of scales bordering the rostral, the Negros, Cebu, and Lubang populations are differentiated from the Samar and Sibuyan, with the Negros also differing from the Marinduque and Luzon. Mann-Whitney U tests of relative size of tympanic scales show the Samar and Cebu populations each differentiated from all others in this subset and the Negros and Marinduque also differing from the Lubang population. Finally, the Samar population is the only one in which males have well-developed nuchal crests. Thus, the only distinctive character states shared by all of these central and northern Philippine populations are the coloration (in preservative) of the patagium in males and the incomplete keeled figure on the snout.

The population from Mindanao, type locality of *everetti* Boulenger (as restricted by Hennig) and probably of *reticulatus* Günther, resembles populations from the continent and the Greater Sundas in the complete development of the keeled Y on the snout, number of incisors (modal value 5), large tympanic scale, well-developed nuchal crest (except for certain Bornean males), and dark pattern on the patagium (table 7). However, the Mindanao population has significantly more supralabials ($P < .05$, pair-wise $t$ tests) and a much larger tympanic scale ($P < .002$, Mann-Whitney U tests) than all of these and significantly more scales around the rostral than the Bornean and Javan populations, but fewer than the continental ones ($P < .05$, $t$ tests). It also differs from all of these populations (except a portion of the Bornean sample) in having a long flexible supraciliary horn. In summary, although the Mindanao population has many of the general features of populations from the continent and Greater Sundas, there are also conspicuous differences. It also shares some characteristics of certain central and northern Philippine populations: high nuchal crest counts with Samar; high supralabial counts with Marinduque, Lubang, and Luzon; and five incisors with Negros, Cebu, and Sibuyan (table 8). Thus, despite its geographic intermediacy, the Mindanao population is not simply a morphological intermediate between populations to the south and west of it on the one hand, and those to the north of it on the other.

The sample from Borneo, which contains the type localities of *cornutus* Günther and *gracilis* Barbour, is complex. As noted earlier (p. 20), males show a distinct bimodal distribution of nuchal crest scale counts. This division into two types corresponds to another involving the flexible supraciliary "horn," which is found only in those Bornean males having low (0 to 4) nuchal crest counts. We consequently have two morphotypes of Bornean males: (1) crested (nuchal crest scales 9 to 16), hornless, and (2) crestless, horned. The distributions of these types among the local samples examined from Borneo are mutually exclusive. Females lacking the supraciliary horn occur only in the samples containing hornless, crested males, and those having well-developed horns, only with corresponding males. Aside from the difference in nuchal crests and supraciliary scales, the only other difference between these two Bornean types is a slight one in relative length of the dewlap (horned males, mean .30 ± .003, hornless males, .33 ± .004; $P < .01$, Mann-Whitney U test). The hornless Bornean morphotype resembles continental, Sumatran, and Javan lizards in that feature; it is also like those populations and the Mindanao population in the development of the nuchal crest. Since the Mindanao population has well-developed supraciliary horns, each Bornean morphotype shares one of its distinguishing character states with the Mindanao population.

Hornless Bornean lizards examined are from four localities in a small corner of the coastal portion of the First Division, Sarawak: Kuching (lat. 1°33′ N, long. 110°20′ E), Matang (lat. 1°36′ N, long. 110°11′ E), Mt. Lundu (lat. 1°41′ N, long. 109°50′ E), and Mt. Poeh (lat. 1°50′ N, long. 109°39′ E). The horned Bornean lizards are from widely separated localities in Sabah, Kalimantan, and Sarawak, including two very close to the First Division localities mentioned above: Santubong (lat. 1°44′ N, long. 110°20′ E), Tanjong Batu (lat. 1°41′ N, long. 110°8′ E). The apparent restriction of the first type to a narrow area that has been under heavy cultivation a long time and includes the most important commercial site in Sarawak suggests that the hornless variety may be a relatively recent introduction.

*Feature 3.*—No other species varies as much in coloration as does the *volans* group. At most, modest variation in brightness (see *obscurus* above, p. 11) or pattern of the trunk (see *fimbriatus*, p. 15) is seen. Nor does any other species show variation in carination, pattern, and size of scales equivalent to that of the *volans* group in development of a nuchal crest, supraciliary horn, and keeled Y on the snout. Quantitative characters also reveal the *volans* group to be more variable than other species. Comparison of variation in the *volans* group with that in other species uses calculations generated by principal components analysis (see Methods). Factor scores for the first three principal components were used to calculate euclidean distances for all pairs of conspecific individuals, with the results shown in Table 9. Mean intraspecific distance for the *volans* group is the largest and differs significantly ($t > 2.28$, $P < .05$) from that of all other species for which sample sizes were adequate.

In terms of variation in these quantitative characters, are the populations of the *volans* group acting as a number of species? Using the same individual factor scores, I calculated the distance in the principal components matrix for all interpopulational pairs of individuals for all pairs of populations of the *volans* group. For this purpose, the two morphotypes on Borneo (see above) were treated as separate populations. Mean distances for all pairs of populations varied from .6751 to 2.7298. The mean of means is 1.3679 ± .0519 (N = 66). Analogous calculations

TABLE 9. Euclidean distance in three-dimensional matrix of principal components scores (see text) for all pairs of conspecific males of species of *Draco*.

| **Species** | **No. of individuals** | **No. of pairs** | **Distance (mean + SE)** |
|---|---|---|---|
| *volans* | 154 | 11,781 | 1.2890 ± .0062 |
| *bimaculatus* | 10 | 45 | .7046 ± .0548 |
| *blanfordi* | 22 | 231 | .9576 ± .0276 |
| *dussumieri* | 10 | 45 | 1.0496 ± .0666 |
| *fimbriatus* | 14 | 91 | 1.0033 ± .0517 |
| *haematopogon* | 15 | 105 | .7888 ± .0271 |
| *lineatus* | 16 | 120 | .8631 ± .0426 |
| *maculatus* | 18 | 153 | .7761 ± .0294 |
| *maximus* | 28 | 378 | .9696 ± .0227 |
| *melanopogon* | 51 | 1,275 | .9157 ± .0123 |
| *obscurus* | 22 | 231 | .6932 ± .0210 |
| *quinquefasciatus* | 45 | 990 | .8923 ± .0146 |
| *taeniopterus* | 8 | 28 | .8737 ± .0843 |

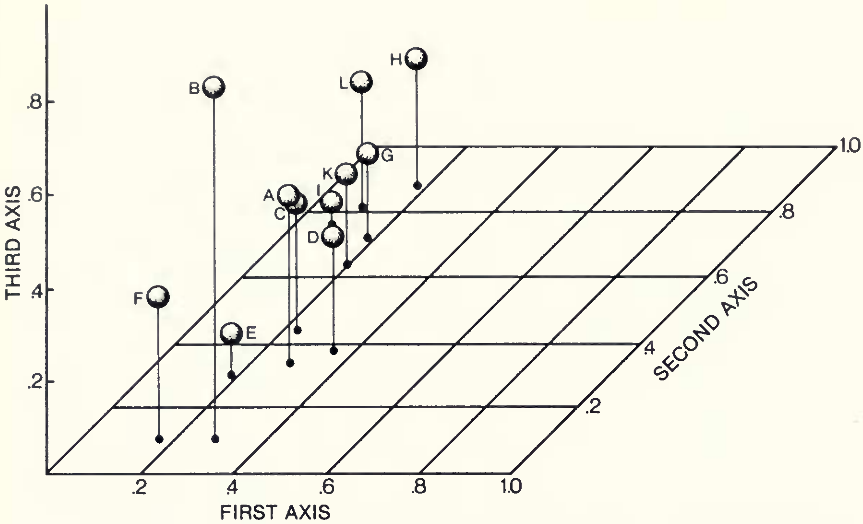


FIG. 3. Males of *Draco volans* group plotted by mean intrapopulation scores of same axes as in Figure 2 and same procedure for standardization. $\overline{X}_i$ equals mean score for population i. $\overline{X}_{min}$ and $\overline{X}_{max}$ have same values as in Figure 2. Populations labeled are: Luzon (A), Lubang (B), Sibuyan (C), Marinduque (D), Negros (E), Samar (F), Cebu (G), Mindanao (H), Borneo "horned" (I), West Malaysia (K), and Java (L). For the sake of clarity, Borneo "hornless" has been omitted from the figure. Relative to I, its position would be slightly to the left on the first axis, almost at the same level on the second, and lower on the third.

were made for interspecific pairs of individuals for all pairs of species excluding the *volans* group. Mean interspecific differences ranged from .9144 to 3.3659. The mean of means was 2.0642 ± .0807 (N = 55), which is significantly ($P < .001$) larger than the corresponding value for the *volans* group. A plot (fig. 3) was made of the mean positions of the *volans* populations in terms of the principal components axes in the same manner as in Figure 2. The scatter of populations is considerable, though not as extensive as that in Figure 2.

Consequently, it appears that, although the *volans* group is internally more variable than any other species, its interpopulational variation is not at the interspecific level usual for the genus. For that reason, it is treated here (see Species Recognized, p. 11) as a single, though complex, species.

## ECOLOGICAL OBSERVATIONS

### STRATIFICATION

This analysis is confined to data (table 10) from three principal collecting stations only 180 km apart in Borneo, as the environments and collecting methods were generally alike at these sites (Inger, 1979). The highly significant difference among species in vertical distribution shown in Table 11 (species × height) is mainly a result of the difference between *melanopogon* and *quinquefasciatus* on the one hand, and the four less abundant species on the other, as Bacon (1970) pointed out. If the data for these two groups of species are separated for analysis, the species × height component is not statistically significant: for *melanopogon* vs. *quin-*

TABLE 10. Vertical distribution of six species of *Draco* captured at three lowland rain forest sites in Borneo.

| | *melanopogon* | | *quinquefasciatus* | | *maximus* | | *volans* | | *obscurus* | | *haematopogon* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Height** | **Male** | **Female** | **Male** | **Female** | **Male** | **Female** | **Male** | **Female** | **Male** | **Female** | **Male** | **Female** |
| *Nanga Tekalit* | | | | | | | | | | | | |
| 1–3 m | 78 | 40 | 46 | 32 | | | | 2 | 10 | 1 | | |
| 3.1–6 m | 158 | 77 | 103 | 65 | 4 | 1 | 1 | 1 | 32 | 5 | | |
| 6.1–9 m | 128 | 66 | 87 | 81 | 9 | 6 | 2 | | 45 | 7 | | |
| 9.1 + m | 30 | 15 | 27 | 17 | 3 | 2 | 1 | | 25 | 5 | | |
| *Pesu* | | | | | | | | | | | | |
| 1–3 m | 14 | 10 | 4 | 5 | 1 | 1 | | | 2 | 1 | | |
| 3.1–6 m | 85 | 45 | 54 | 26 | | | 1 | 3 | 4 | 1 | 3 | 1 |
| 6.1–9 m | 89 | 47 | 50 | 34 | 8 | 5 | 5 | 7 | 5 | 3 | 9 | 4 |
| 9.1 + m | 21 | 6 | 13 | 10 | 2 | 2 | 2 | | 5 | 4 | 2 | 1 |
| *Labang* | | | | | | | | | | | | |
| 1–3 m | 9 | 6 | 5 | 10 | | | | | | | | 1 |
| 3.1–6 m | 50 | 23 | 25 | 13 | 2 | 3 | 4 | 2 | | | 7 | 3 |
| 6.1–9 m | 19 | 10 | 12 | 9 | 5 | 1 | 2 | 1 | | | 2 | 5 |
| 9.1 + m | 1 | 2 | | | 1 | | 1 | 1 | | | 1 | 1 |
| Max. capture height | 12 m | | 15 m | | 11 m | | 11 m | | 14 m | | 12 m | |

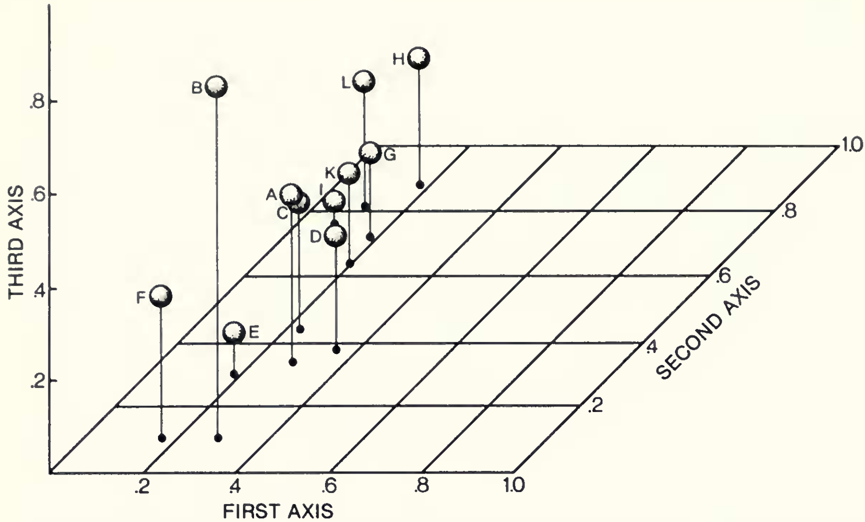


FIG. 3. Males of *Draco volans* group plotted by mean intrapopulation scores of same axes as in Figure 2 and same procedure for standardization. $\overline{X}_i$ equals mean score for population i. $\overline{X}_{min}$ and $\overline{X}_{max}$ have same values as in Figure 2. Populations labeled are: Luzon (A), Lubang (B), Sibuyan (C), Marinduque (D), Negros (E), Samar (F), Cebu (G), Mindanao (H), Borneo "horned" (I), West Malaysia (K), and Java (L). For the sake of clarity, Borneo "hornless" has been omitted from the figure. Relative to I, its position would be slightly to the left on the first axis, almost at the same level on the second, and lower on the third.

were made for interspecific pairs of individuals for all pairs of species excluding the *volans* group. Mean interspecific differences ranged from .9144 to 3.3659. The mean of means was 2.0642 ± .0807 (N = 55), which is significantly ($P < .001$) larger than the corresponding value for the *volans* group. A plot (fig. 3) was made of the mean positions of the *volans* populations in terms of the principal components axes in the same manner as in Figure 2. The scatter of populations is considerable, though not as extensive as that in Figure 2.

Consequently, it appears that, although the *volans* group is internally more variable than any other species, its interpopulational variation is not at the interspecific level usual for the genus. For that reason, it is treated here (see Species Recognized, p. 11) as a single, though complex, species.

## ECOLOGICAL OBSERVATIONS

### STRATIFICATION

This analysis is confined to data (table 10) from three principal collecting stations only 180 km apart in Borneo, as the environments and collecting methods were generally alike at these sites (Inger, 1979). The highly significant difference among species in vertical distribution shown in Table 11 (species × height) is mainly a result of the difference between *melanopogon* and *quinquefasciatus* on the one hand, and the four less abundant species on the other, as Bacon (1970) pointed out. If the data for these two groups of species are separated for analysis, the species × height component is not statistically significant: for *melanopogon* vs. *quin-*

Table 10. Vertical distribution of six species of *Draco* captured at three lowland rain forest sites in Borneo.

| Height | *melanopogon* | | *quinquefasciatus* | | *maximus* | | *volans* | | *obscurus* | | *haematopogon* | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Male | Female | Male | Female | Male | Female | Male | Female | Male | Female | Male | Female |
| *Nanga Tekalit* | | | | | | | | | | | | |
| 1–3 m | 78 | 40 | 46 | 32 | | | | 2 | 10 | 1 | | |
| 3.1–6 m | 158 | 77 | 103 | 65 | 4 | 1 | 1 | 1 | 32 | 5 | | |
| 6.1–9 m | 128 | 66 | 87 | 81 | 9 | 6 | 2 | | 45 | 7 | | |
| 9.1 + m | 30 | 15 | 27 | 17 | 3 | 2 | 1 | | 25 | 5 | | |
| *Pesu* | | | | | | | | | | | | |
| 1–3 m | 14 | 10 | 4 | 5 | 1 | 1 | | | 2 | 1 | | |
| 3.1–6 m | 85 | 45 | 54 | 26 | | | 1 | 3 | 4 | 1 | 3 | 1 |
| 6.1–9 m | 89 | 47 | 50 | 34 | 8 | 5 | 5 | 7 | 5 | 3 | 9 | 4 |
| 9.1 + m | 21 | 6 | 13 | 10 | 2 | 2 | 2 | | 5 | 4 | 2 | 1 |
| *Labang* | | | | | | | | | | | | |
| 1–3 m | 9 | 6 | 5 | 10 | | | | | | | | 1 |
| 3.1–6 m | 50 | 23 | 25 | 13 | 2 | 3 | 4 | 2 | | | 7 | 3 |
| 6.1–9 m | 19 | 10 | 12 | 9 | 5 | 1 | 2 | 1 | | | 2 | 5 |
| 9.1 + m | 1 | 2 | | | 1 | | 1 | 1 | | | 1 | 1 |
| Max. capture height | 12 m | | 15 m | | 11 m | | 11 m | | 14 m | | 12 m | |

TABLE 11. Analysis of distribution of capture height for six species of *Draco* presented in Table 10.

| Source | G* | Degrees of freedom | *P* |
|---|---|---|---|
| Species × height | 84.802 | 15 | .001 |
| Species × sex | 39.862 | 5 | .001 |
| Height × sex | 4.890 | 3 | .10 |
| Interaction | 10.560 | 15 | .50 |
| Species × height × sex | 140.114 | 38 | .001 |
| Species × height | 84.802 | 15 | .001 |
| Species × locality | 177.970 | 10 | .001 |
| Locality × height | 86.720 | 6 | .001 |
| Interaction | 41.594 | 30 | .07 |
| Species × height × locality | 391.086 | 61 | .001 |

*G test described in Sokal & Rohlf (1969).

*quefasciatus,* G equals 4.29 (df = 3, $P > .20$), and for the other group of four, G equals 15.39 (df = 9, $P = .08$). The first two species were generally caught at lower heights (55% of *melanopogon* and *quinquefasciatus* at 6 m or lower) than the others (66% above 6 m). However, Bacon's (1970) observations made from tree platforms, most of which were higher than any capture height, do not agree with the impression of stratification derived from capture data. Every one of these species moves through all levels of the canopy, and one-sixth of Bacon's 172 observations of *Draco* from platforms were of individuals at heights exceeding 36 m.

Vertical distribution of the same species (excluding *haematopogon*) at several forest localities in Selangor, Malaya, is lower than that shown in Table 10. Less than 5% of the 383 individuals collected by us in Malaya were at levels higher than 6 m, in contrast to 47% of the Bornean lizards. This difference is almost certainly an artifact of collection method; blow guns were the only available weapons in Malaya.

In northeastern Thailand, *D. maculatus* were caught from ground level to 15 m (Inger & Colwell 1977), the height frequency distribution being: < 1 m, 10; 1–3 m, 2; 3–6 m, 10; 6–9 m, 21; > 9 m, 13. Six of the lizards caught on the ground were hatchlings. The similarity of this distribution to those of the Bornean species suggests that the pattern is probably common to all species living in well-developed forest.

## SUBSTRATE

Almost all the *Draco* collected or observed by us in Borneo, Malaya, and Thailand were using tree trunks or branches as their substrate. At three localities from which we have adequate data, *Draco* clearly showed a bias toward larger trees as perch sites (table 12). Although measurements of trees used by *Draco* were not recorded at the Bornean localities, the lizards observed at great heights by Bacon (1970) at those places had to be on very large trees.

## DIETS

Although species of *Draco* do feed, as Smith (1935) put it, "on insects, grubs, etc.," ants appear to be the principal component of the diets, at least in rain forest species. Between 88% and 100% of the stomachs examined from four coexisting

TABLE 12. Size of trees on which *Draco* were caught at three sites compared with tree size distribution in vegetation samples at those sites (descriptions of environments given in Inger, 1979; all species of *Draco* combined).

| | Thailand | | Malaya | | | |
|---|---|---|---|---|---|---|
| | Sakaerat* | | Bukit Lanjan** | | Ulu Gombak† | |
| Tree diameter (DBH cm) | *Draco* | Vegetation sample | *Draco* | Vegetation sample | *Draco* | Vegetation sample |
| 11 | 2 | 370 | 17 | 75 | 14 | 36 |
| 11–30 | 28 | 323 | 118 | 57 | 46 | 36 |
| 31–60 | 14 | 56 | 64 | 14 | 55 | 6 |
| 60 | 2 | 11 | 24 | 6 | 28 | 2 |
| | 46 | 760 | 231 | 152 | 152 | 80 |
| | chi square = 47.8 | | chi square = 90.5 | | chi square = 66.9 | |

*Dry evergreen forest. **Old selectively logged rain forest. †Primary hill rain forest.

species contained ants, which accounted for 59% to 99% of prey items (table 13). Two of these species, *melanopogon* and *obscurus*, fed heavily on termites, which occurred in 44% to 52% of their stomachs and made up 23% to 40% of prey items (table 13). Marked, statistically significant differences occur among these four species in size-frequency distribution of prey (table 14), whether ants and termites are treated separately or all prey are grouped into one 4 × 4 contingency table (chi square > 150). However, these statistical differences do not appear to have biological significance. The largest species, *maximus*, has a disproportionate number of small and very large prey, and the smallest species, *melanopogon*, a disproportionately large number of medium-sized prey.

These unexpected results are probably related to the strongly clumped distribution of the principal prey organisms, which may allow the contents of one stomach to distort prey size distribution. For example, one stomach of *maximus* accounted for 63% of the 478 ants in the smallest size category (table 14). A single stomach of *obscurus* held 50% of that species' 186 termites in the 3- to 5-mm range. To avoid this distorting influence, tests of the differences among species within prey size categories were made applying the Kruskal-Wallis analysis of variance (Siegel, 1956) to the stomachs ranked according to the number of prey items of that particular category. The null hypothesis of no differences among species was rejected for the two smallest prey size categories (table 15). With this analysis of

TABLE 13. Taxonomic composition of prey of four coexisting species of *Draco*.

| Species | Ants | Termites | Beetles | Centipedes | Lepidoptera | Other | Total |
|---|---|---|---|---|---|---|---|
| | | | | NO. OF STOMACHS | | | |
| *maximus* | 24 | 0 | 2 | 3 | 1 | 2 | 24 |
| *obscurus* | 25 | 13 | 0 | 1 | 0 | 0 | 25 |
| *quinquefasciatus* | 25 | 2 | 1 | 0 | 1 | 0 | 25 |
| *melanopogon* | 22 | 11 | 3 | 0 | 5 | 0 | 25 |
| | | | | NO. OF ITEMS | | | |
| *maximus* | 836 | 0 | 2 | 3 | 1 | 2 | 844 |
| *obscurus* | 659 | 200 | 0 | 1 | 0 | 0 | 860 |
| *quinquefasciatus* | 702 | 30 | 1 | 0 | 1 | 0 | 734 |
| *melanopogon* | 922 | 617 | 3 | 0 | 7 | 1 | 1,550 |

TABLE 14. Size distribution of prey of four coexisting species of *Draco*.

| Prey size | *maximus* | *obscurus* | *quinquefasciatus* | *melanopogon* |
|---|---|---|---|---|
| *Ants* | | | | |
| < 3 mm | 478 | 214 | 435 | 269 |
| 3–5 mm | 193 | 346 | 149 | 574 |
| 5–10 mm | 134 | 99 | 114 | 78 |
| > 10 mm | 31 | . . . | 4 | 1 |
| Subtotal | 836 | 659 | 702 | 922 |
| *Termites* | | | | |
| < 3 mm | . . . | 5 | . . . | 31 |
| 3–5 mm | . . . | 186 | 7 | 582 |
| 5–10 mm | . . . | 9 | 23 | 4 |
| Subtotal | | 200 | 30 | 617 |
| *Other arthropods* | | | | |
| < 5 mm | 2 | 1 | 1 | 7 |
| 5–10 mm | 1 | . . . | 1 | 4 |
| > 10 mm | 5 | . . . | . . . | . . . |
| Subtotal | 8 | 1 | 2 | 11 |
| TOTAL | 844 | 860 | 734 | 1,550 |

ranks, the smallest species, *melanopogon*, is at or near the top in consumption of the two smallest prey categories, while the largest species, *maximus*, is at the bottom. The order is reversed for the larger prey categories.

Because *melanopogon* and *quinquefasciatus* tend to occur together in relatively low levels of the forest (see above), comparison of these two was carried out separately by means of Mann-Whitney U tests (Siegel, 1956). Again stomachs were ranked according to number of prey within prey size categories. The only statistically significant difference between these species involved prey in the 3- to 5-mm range (table 15), with *melanopogon* consuming more. Comparing prey size of *obscurus* and *maximus*, which are more abundant at higher levels (see above), in the same way gives almost identical results (table 15). These two do not differ in consumption of prey in the < 3-mm and 4- to 10-mm categories, but differ significantly in use of prey in the 3- to 5-mm range, with *obscurus* consuming more. *Draco maximus* differs from *obscurus* and the others in its use of the largest prey (table 14).

*Draco maculatus* in northeastern Thailand appears to have a diet similar to that of the rain forest species. Eight of 10 stomachs examined contained ants, which comprised 96% of all prey items. Other prey included lepidopteran larvae, centipedes, and orthopterans.

## Relative Abundance

Large collections of *Draco* made in rain forests at the three main stations in Borneo (Inger, 1979) include seven species altogether, but only six at any one place (table 16). Although absolute numbers obtained differ widely from place to place, abundance ranks vary only moderately. *Draco melanopogon* and *quinquefasciatus* were the first and second most numerous, respectively, at all three localities, though their preeminence in collections may be an artifact of their occurrence in lower strata which would make them more susceptible to capture. Two species, *obscurus* and *haematopogon*, exhibited major interlocality differences in abundance which are not easily understood, as all three environments were well-developed

TABLE 15. Rank order comparisons among species of *Draco* within prey size categories.

| | Prey size | | | |
|---|---|---|---|---|
| | < 3 mm | 3–5 mm | 5–10 mm | > 10 mm* |
| | | 4-WAY TESTS | | |
| H** | 8.22 | 32.31 | 3.60 | . . . |
| P | .05 | .001 | .30 | . . . |
| Highest† | *quinquefasciatus* | *melanopogon* | *obscurus* | *maximus* |
| Second | *melanopogon* | *obscurus* | *maximus* | |
| Third | *obscurus* | *quinquefasciatus* | *quinquefasciatus* | |
| Lowest | *maximus* | *maximus* | *melanopogon* | |
| | | PAIR-WISE TESTS | | |
| *melanopogon* × *quinquefasciatus* | | | | |
| Z‡ | 1.70 | 4.64 | .29 | . . . |
| P | .08 | .001 | .78 | . . . |
| *maximus* × *obscurus* | | | | |
| Z‡ | .84 | 2.86 | .04 | . . . |
| P | .40 | .004 | .95 | . . . |

*Tests of differences among species were not carried out on this size category because only *maximus* fed on it to any appreciable extent. Prey of this size were found in 14 stomachs of *maximus*, one each of *melanopogon* and *quinquefasciatus*, and none of *obscurus*.
**H of Kruskal-Wallis analysis of variance (Siegel, 1956). †Highest = species with greatest cumulative ranking within given prey size categories. ‡Z of Mann-Whitney test (Siegel, 1956).

forests. One might speculate that the flat topography at Labang (Inger, 1979), by increasing soil moisture, was unfavorable for oviposition or development of embryos of *obscurus*, but I have no data to support this suggestion. There is no evident reason for the rarity of *haematopogon* in the sample from Nanga Tekalit. If these populations experience stochastic variation in numbers, speculation about deterministic causes is not warranted.

In fact, there is some evidence for stochastic variation. Intraspecific evaluation of interlocality differences in relative abundances (table 16) was made by means of arcsin tests (Sokal & Rohlf, 1969). For this purpose, relative abundances were

TABLE 16. Abundances of species of *Draco* at three rain forest sites* in Borneo.

| | No. of individuals | | | Relative abundance** | | |
|---|---|---|---|---|---|---|
| Species | Nanga Tekalit | Pesu | Labang | Nanga Tekalit | Pesu | Labang |
| *melanopogon* | 654 | 339 | 125 | .2191 | .2555 | .1277 |
| *quinquefasciatus* | 579 | 203 | 78 | .2118 | .1530 | .0793 |
| *obscurus* | 138 | 28 | 0 | .0505 | .0211 | 0 |
| *maximus* | 29 | 22 | 13 | .0106 | .0166 | .0133 |
| *volans* | 8 | 18 | 11 | .0029 | .0136 | .0112 |
| *haematopogon* | 1 | 20 | 20 | .0004 | .0151 | .0204 |
| *fimbriatus* | 0 | 0 | 2 | 0 | 0 | .0020 |
| TOTALS | 1,409 | 630 | 249 | 2,789 | 1,327 | 978 |

*Sites located and described in Inger (1979). **Abundance relative to lizards of all families collected at each site.

calculated on the basis of the entire collection of all families of lizards at each site in order to minimize the arithmetic, nonbiological compensation of proportions when one is reduced. No tests were run on *fimbriatus* because of the small numbers caught. Of the 18 possible tests, 13 show significant ($P < .05$) interlocality differences, and *maximus* is the only species lacking such differences. On the basis of chance alone, given 18 tests and using a significance level of $P = .05$, at least one test should have reached that level. However, chance cannot explain 13 of 18. If the same kind of tests are run using the total number of *Draco* collected as the base of proportions, 12 of the 18 interlocality differences reach statistically significant levels. Important shifts in relative abundance of a particular species do not appear to be the inverse of shifts in other species, which would be expected if competition accounts for the differences between localities. The only exception to this statement involves the interlocality rank orders for *haematopogon* and *obscurus;* however, as they occur in about equal numbers at one locality, even suggestive evidence for competition between them is not strong.

## Ecological Summary

In any area of rain forest in Borneo, Sumatra, or the southern part of the Malay Peninsula, five to seven species of *Draco* coexist, though the composition of the assemblages varies slightly (table 17). Differences among the assemblages are in one instance the result of geographical limits of species' distributions: *blanfordi* has rarely been found south of the Thai-Malayan border (ca. lat. 6°N), and *taeniopterus,* never (Hennig, 1936). Geographic limits do not explain the other intersite differences. *Draco haematopogon* occurs in Sumatra and Malaya (Hennig, 1936) and *cristatellus* is known from Borneo and Malaya (p. 1). The two Bornean localities at which *fimbriatus* was not obtained have forests and topography similar to those at the Malayan sites.

The number of species present at any one place does not result from ignoring altitudinal stratification. Gunong Benom (table 17), which extends from 180 to 1,800 m, seems to offer the best opportunity for such specialization, yet all seven of the species from there were caught in the lowest 65 m (Grandison, 1972). At the Labang site, total topographical relief was less than 200 m.

In other respects, the species of *Draco* in this rain forest belt exhibit only moderate ecological specialization. Two, *melanopogon* and *quinquefasciatus,* tend to be more abundant in lower forest strata (p. 24), and two, *melanopogon* and *obscurus,* tend to eat more termites and more prey in the 3- to 5-mm range (p. 27). Nonetheless, ranges of utilization of resources of coexisting species overlap widely.

One possible conclusion to be drawn from the co-occurrence of many species at many places is that, despite broad overlapping in resource utilization, they are not competing. If this hypothesis is correct, we have still to learn what ecological processes keep these populations below the level at which they might compete. An alternative hypothesis is that we have yet to discover the ecological dimension along which these species do segregate. Available data do not permit a choice between these hypotheses.

TABLE 17. Assemblages of species of *Draco* collected at various localities.*

| Species | Thailand | West Malaysia | | | Sumatra | Sarawak | | |
|---|---|---|---|---|---|---|---|---|
| | Khao Chong lat. 7°30′ N | Bukit Lanjan lat. 3°11′ N long. 101°37′ E | Ulu Gombak lat. 3°22′ N long. 101°47′ E | Gunong Benom lat. 3°50′ N long. 102°6′ E | Bukit Lawan lat. 3°30′ N long. 98°12′ E | Nanga Tekalit lat. 1°37′ N long. 113°35′ E | Pesu lat. 3°7′ N long. 113°48′ E | Labang lat. 3°21′ N long. 113°27′ E |
| *blanfordi* | + | | | | | | | |
| *cristatellus* | + | | | + | + | | | |
| *fimbriatus* | + | + | + | + | + | | | + |
| *haematopogon* | | | | | | + | + | + |
| *maximus* | | | + | + | | + | + | + |
| *melanopogon* | + | + | + | + | + | + | + | + |
| *obscurus* | + | + | + | + | + | + | + | |
| *quinquefasciatus* | | + | + | + | + | + | + | + |
| *taeniopterus* | + | | | | | | | |
| *volans* | + | + | | + | + | + | + | + |

*The list from Gunong Benom was taken from Grandison (1972). Except for the record of *cristatellus* (=*punctatus* of Grandison and Taylor) from Khao Chong (Taylor, 1963), all other occurrences were verified by examination of specimens.

## ACKNOWLEDGMENTS

Curators at a number of museums were generous in making specimens available and very tolerant of my slowness in returning their material. In this connection I want to thank especially A. G. C. Grandison (BM), C. J. McCoy (CM), A. E. Leviton (CAS), E. E. Williams (MCZ), G. R. Zug (USNM), and R. G. Zweifel (AMNH).

At several stages of development of the manuscript, helpful criticism was provided by W. R. Heyer (USNM) and H. K. Voris (FMNH), and I am grateful to them. I also appreciate the generosity of C. J. M. Musters in making his manuscript available to me well in advance of publication. Several members of the staff of Field Museum provided important technical assistance, in particular M. Moskovitz, M. Ozaki, and A. Resetar.

Fieldwork was supported by National Science Foundation grants G 20867, GB 1049, and GB 7845X.

## LITERATURE CITED

Bacon, J. P., Jr. 1970. Local and latitudinal variation in reptiles and amphibian community structure in East Asia. Ph.D. thesis, University of Chicago, Chicago, 141 pp.

Boulenger, G. A. 1887. On new reptiles and batrachians from North Borneo. Ann. Mag. Nat. Hist., ser. 5, **20:** 95–97.

———. 1900. Descriptions of new batrachians and reptiles from the Larut Hills, Perak. Ann. Mag. Nat. Hist., ser. 7, **6:** 186–193.

Flower, S. S. 1896. Notes on a collection of reptiles and batrachians made in the Malay Peninsula in 1895–96; with a list of the species recorded from that region. Proc. Zool. Soc. London, **1896:** 856–916.

Grandison, A. G. C. 1972. The Gunong Benom Expedition 1967. 5. Reptiles and amphibians of Gunong Benom with a description of a new species of *Macrocalamus*. Bull. Br. Mus. (Nat. Hist.) Zool., **23:** 45–101.

Hairston, N. G. 1957. Observations on the behavior of *Draco volans* in the Philippines. Copeia, **1957:** 262–265.

Hennig, Willi. 1936. Revision der Gattung *Draco* (Agamidae). Temminckia, **1:** 153–220.

Inger, R. F. 1979. Abundance of amphibians and reptiles in tropical forests of Southeast Asia. University of Hull, Dept. of Geography, Misc. Ser. No. 22: 93–110.

Inger, R. F., and R. K. Colwell. 1977. Organization of contiguous communities of amphibians and reptiles in Thailand. Ecol. Monogr., **47:** 229–253.

Leviton, A. E., R. McDiarmid, S. Moody, M. Nickerson, J. Rosado, O. Sokol, and H. Voris. 1980. Museum acronyms. Herpetol. Rev., **11:** 93–102.

Nie, N. H., C. H. Hull, J. G. Jenkins, K. Steinbrenner, and D. H. Bent. 1975. Statistical Package for the Social Sciences. 2nd ed. McGraw-Hill, New York.

Siegel, Sidney. 1956. Nonparametric Statistics for the Behavioral Sciences. McGraw-Hill, New York.

Smith, M. A. 1935. Fauna of British India. Reptilia and Amphibia. Vol. II. Taylor and Francis, London.

———. 1937. *Draco blanfordi* and its allies. Bull. Raffles Mus., **13:** 75–76.

Sokal, R. R., and F. J. Rohlf. 1969. Biometry. W. H. Freeman, San Francisco.

Taylor, E. H. 1922. The Lizards of the Philippine Islands. Bureau of Printing, Manila.

———. 1963. The lizards of Thailand. Univ. Kansas Sci. Bull., **44:** 687–1077.

APPENDIX. Summary of quantitative data on species of *Draco* (definitions of characters given in Materials and Methods).

| | Snout-vent | | | | | | Supralabials | | | Scales bordering rostral | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | ♂ | | | ♀ | | | | | | | | |
| Species | N | Range | $\bar{X} \pm SE$ | N | Range | $\bar{X} \pm SE$ | N | Range | $\bar{X} \pm SE$ | N | Range | $\bar{X} \pm SE$ |
| *melanopogon* | 83 | 69–84 | 76.59 ± .38 | 23 | 71–86 | 79.39 ± .95 | 71 | 10–15 | 12.20 ± .13 | 58 | 6–12 | 9.26 ± .15 |
| *haematopogon* | 29 | 61–77 | 70.05 ± .64 | 7 | 71–81 | 76.37 ± 1.03 | 36 | 10–13 | 11.22 ± .13 | 19 | 6–9 | 7.84 ± .24 |
| *mindanensis* | 8 | 89–107 | 95.38 ± 1.99 | 2 | 89–107 | 98.0 | 13 | 11–15 | 13.38 ± .31 | 13 | 6–10 | 8.23 ± .38 |
| *maximus* | 29 | 117–139 | 131.03 ± .89 | 12 | 114–137 | 124.17 ± 2.36 | 43 | 12–18 | 14.56 ± .20 | 36 | 8–12 | 9.53 ± .18 |
| *quinquefasciatus* | 57 | 81–110 | 91.39 ± .75 | 13 | 93–107 | 97.69 ± 1.36 | 54 | 10–17 | 12.98 ± .18 | 52 | 6–12 | 8.75 ± .17 |
| *dussumieri* | 13 | 70–79 | 74.81 ± .80 | 7 | 80–92 | 85.50 ± 1.57 | 13 | 9–12 | 10.85 ± .25 | 13 | 5–9 | 7.31 ± .27 |
| *obscurus* | 37 | 75–113 | 85.58 ± 1.27 | 11 | 78–86 | 81.68 ± .90 | 38 | 7–11 | 9.23 ± .14 | 19 | 5–7 | 5.84 ± .14 |
| *taeniopterus* | 22 | 66–80 | 73.82 ± .86 | 5 | 68–76 | 72.20 ± 1.50 | 35 | 7–11 | 8.17 ± .15 | 10 | 5–7 | 6.50 ± .22 |
| *blanfordi* | 18 | 102–131 | 119.10 ± 1.81 | 5 | 106–117 | 110.20 ± 1.93 | 28 | 7–11 | 8.96 ± .17 | 26 | 6–9 | 7.42 ± .17 |
| *fimbriatus* | 24 | 97–132 | 108.02 ± 1.53 | 16 | 95–119 | 105.86 ± 1.55 | 44 | 9–14 | 11.61 ± .17 | 42 | 4–10 | 7.05 ± .21 |
| *cristatellus* | 10 | 70–90 | 83.20 ± 2.01 | 3 | 79–88 | 82.4 | 13 | 9–12 | 10.08 ± .26 | 12 | 5–7 | 6.33 ± .28 |
| *maculatus* | 30 | 62–86 | 73.58 ± 1.27 | 3 | 69–74 | 71.8 | 31 | 7–11 | 9.00 ± .17 | 31 | 3–7 | 5.26 ± .16 |
| *bimaculatus* | 16 | 61–71 | 65.00 ± .82 | 7 | 58–67 | 64.79 ± 1.25 | 18 | 8–10 | 8.89 ± .16 | 18 | 4–6 | 5.11 ± .20 |
| *lineatus* | 17 | 59–78 | 69.38 ± 1.65 | 6 | 69–79 | 72.83 ± 1.62 | 22 | 4–8 | 6.18 ± .24 | 22 | 4–9 | 6.23 ± .28 |
| *volans* | 180 | 59–82 | 70.72 ± .94 | 73 | 64–91 | 76.77 ± .65 | 271 | 7–12 | 9.33 ± .07 | 241 | 3–8 | 5.19 ± .08 |